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Allometry and Size Evolution in the Rattlesnake, with Emphasis on Predatory Strike Performance

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Allometry and Size Evolution in the Rattlesnake, with Emphasis on Predatory Strike Performance

by

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Dedication

To my wife, Veronica, for her unwavering support, love, and tolerance of this big kid

and

To Carl Baertlein, whose wit and strength in the face of adversity inspires me to make the most out of every single day

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Now I'm going roadcruising….

Allometry and Size Evolution in the Rattlesnake, with Emphasis on Predatory Strike Performance

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Changes in body size have significant implications for an animal's morphology and physiology, with such ontogenetic or evolutionary changes affecting surface-to-volume ratios, metabolic rates, and kinematics (body movements exclusive of their underlying forces). The majority of comparative studies on feeding in vertebrates have centered on interspecific comparisons between species of similar ecologies with similarly sized animals and descriptive papers on the feeding in a single species of vertebrate typically focus on restricted size ranges of animals to specifically avoid ontogenetic-based variation. Rattlesnakes (genera *Crotalus* and *Sistrurus*) are an excellent group to investigate the effects of body size on feeding kinematics because of their substantial body size variation and a feeding system uncomplicated by limb movements.

The western diamondback rattlesnake (*C. atrox*) was selected for examining intraspecific body size effects on feeding because of its large intraspecific size variation and local availability. Using preserved specimens, body size was found in to increase isometrically for six out of seven morphological measurements (head volume with negative allometry). Multiple predatory strike sequences were filmed (1000 fps) and analyzed for 20 individual western diamondback rattlesnakes in the lab, with maximum acceleration found to be size independent, contrary to kinematic values predicted based on isometric growth. Predatory and defensive strikes were compared for a small subset of rattlesnakes: maximum acceleration did not vary between strike types, although distances in defense strikes were twice those of predatory strikes.

A phylogenetic estimate was created using a maximum parsimony analysis on 2385 base pairs of sequence data (downloaded from GenBank) and 311 morphological characters (generated for this analysis) for 28 rattlesnake taxa and five outgroup taxa. This estimate served as the backbone for interspecific regression analyses of morphological and feeding variables for six rattlesnake taxa (four *Crotalus* species and two *Sistrurus* species) using independent contrasts to account for historical relatedness. Body scaling relationships similar to those found in *C. atrox* were found in each of the additional five taxa and strike comparisons between adults of the same six species again demonstrated size independence in maximum acceleration of the strike.

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Chapter 1

Allometry and Size Evolution in the Rattlesnake, with Emphasis on Predatory Strike Performance - An Overview

Evolutionary and ontogenetic changes in body size are often accompanied by compensatory changes in metabolism, shape, and locomotor pattern. There are two definitions used to describe the scaling relationship between a given variable and body size, these being definitions of isometry and allometry. Animals growing isometrically maintain the similar shapes although they have increased in size, essentially remaining scale models of each other. In order to maintain these proportions, we would expect, under isometry, that area measurements would increase, as linear measurements increase, proportional to that linear measurement squared. Volume (or mass assuming constant density) under isometry, would be proportional to that linear measurement cubed. Allometry describes changes in shape as size increases. Allometry can be either negative or positive, as the scaling exponent can be different than that predicted under isometry.

In making predictions on how size may affect an animal's kinematics (body movements exclusive underlying forces), researchers refer to the predictions of Hill (1950), collectively known as the Hill model. As animals maintain geometric similarity, or grow isometrically, there are predicted patterns of kinematic scaling with respect to body size. Accelerations are predicted to scale to the inverse of length, whereas velocity and timing variables are expected to demonstrate kinematic similarity. Only a handful of studies have examined the ontogeny of body size as it applies to vertebrate feeding kinematics, as most

comparative studies on feeding in vertebrates have eliminated ontogenetic body size as a variable in favor of comparisons between species with similarly sized adult animals. In the majority of morphological variables in these studies, animal growth was found to be isometric, but no common pattern was seen in the relationship between body size and kinematic variables, with some scaling relationships supporting the Hill model, but others showing deviations from these predictions. As an example, timing variables have been shown to scale isometrically with respect to linear body measurements, but in other studies that scaling coefficient has been reported as .33 and as 0, indicating mass independence of kinematics.

Rattlesnakes display substantial body size variation and are an excellent group in which to investigate the effects of body size on feeding kinematics. With conspicuous rattles at the end of their tails, rattlesnakes are one of the most identifiable ophidian groups found in the New World. There are over 30 species of these venomous snakes distributed throughout different habitats across the Americas, from the xeric North American deserts to the tropical forests of the Amazon Basin and across a wide range of elevations (below sea level to 4000m). These snakes display a large degree of intraspecific variation in body size, which, within some species, ranges over an order in magnitude (Klauber, 1937; Campbell and Lamar, 1989). The variation seen in rattlesnake body sizes is remarkable: rattlesnakes display a wide range of adult lengths with ontogenetic variation spanning two orders of magnitude in several species. Rattlesnakes are also venomous and can deliver a proteolytic and hemotoxic venom through their enlarged maxillary fangs, with an entire predatory strike sequence (typically a rapid strike and release) often lasting less than 0.5 sec.

The combination of a rapid and stereotypic predatory strike and the great range of sizes exhibited both ontogenetically and interspecifically presents an

opportunity to test, in a phylogenetic context, whether changes in body size have imposed constraints on the evolution of rattlesnake strike performance. There are three ways to analyze strike variation: kinematics (motion), dynamics (force), and morphology; I will use both kinematic and morphological methods in this study. Five main questions were investigated using these six rattlesnake species: 1) what are the intraspecific scaling relationships of body size? , 2) for a single species (*Crotalus atrox*), are these relationships accurate predictors of the scaling of strike kinematics, 3) within adults of six rattlesnake species, what are the interspecific scaling relationships of body size and strike kinematics? 4) can intraspecific scaling patterns of body size and strike kinematics for a single species be used to predict interspecific scaling patterns? and 5) do strike performance parameters follow predicted models of kinematic scaling, based on either geometric or functional similarity?

Because my intra- and interspecific comparisons of strike behavior were to be based solely on variables measured during predatory strikes, I was initially concerned that I might not be able to discern between predatory and defensive strikes. Although qualitative behavioral characteristics historically had been used to differentiate between the two types of strikes (i.e., defensive strikes characterized by slow, arcing tongue flicks and a rattling tail), I filmed several strikes in which these qualitative characters were contradictory (both predatory and defensive behaviors observed in single strike). No quantitative data yet existed for comparisons between kinematic strike variables in any species of snake. In Chapter 2, I filmed and compared both strike types (unambiguously assigned) from four *Crotalus atrox*. Maximum acceleration was not statistically different between the strike types, but maximum velocity was approximately 1 m/s faster in defensive strikes. Defensive strike distances were roughly twice

m/s faster in defensive strikes. Defensive strike distances were roughly twice those of predatory strikes with strike distance being correlated with maximum velocity, but not to maximum acceleration.

In Chapter 3, the western diamondback rattlesnake (*Crotalus atrox*) served as the model for investigating both intraspecific morphological and kinematic variation. I examined over 125 preserved specimens taking measures of body length, head dimension, weight, circumference, and volume for each specimen. Isometry was found for most variables, save the measures of the head that demonstrated negative allometry with respect to increasing body size (length or mass). Morphological results satisfied the assumptions of geometric similarity for predictions of the Hill (1950) model to be valid: maximum acceleration should decrease with increased size. In the laboratory with a high-speed camera (1000 frames/sec), I filmed the predatory strikes of twenty individual *C. atrox*. Multiple strikes were recorded for 18 snakes, with maximum performance values attained by a given snake over all of its recorded strikes being used in the analyses. Maximum acceleration was found to be size-independent in contrast to the kinematic predictions of Hill (1950). Velocity increased with increased size and was correlated with strike distance and animal size. Both large and small snakes struck with equivalent maximum accelerations, however, larger snakes struck from further distances and reached higher strike velocities than did small snakes.

To address the potential bias in interpreting interspecific strike comparisons due to issues of historical relatedness, I constructed a phylogenetic estimate of the rattlesnakes that would serve as the template for subsequent interspecific comparisons. Chapter 4 details the construction of this phylogeny based on 2383 molecular characters (four genes, all downloaded from GenBank) and 209 morphological characters (primarily new cranial osteological characters) available for 30 rattlesnake taxa and five outgroup taxa. Using a total evidence

approach (Kluge, 1989), all data were combined and analyzed using maximum parsimony. A single most-parsimonious tree was found with a majority of the species-level and species-group relationships shown in the combined analysis tree also present in trees based on partitions of molecular data alone. Although high levels of intraspecific variation were found in the morphological data set, two synapomorphies were found to unite *Sistrurus catenatus* and *S. miliarius* to the exclusion of *S. ravus*, which is now recognized as a member of genus *Crotalus*. This is the first species-level estimate of the rattlesnakes based on both morphological and molecular data.

In Chapter 5, I performed interspecific comparisons of morphology and kinematic variation from six species of rattlesnakes using the newly created rattlesnake phylogeny as the backbone for independent contrasts. Data for the same morphological variables taken in the intraspecific analysis were taken for an additional 259 preserved museum specimens from five species of rattlesnakes (*C. lepidus, C. viridis, C. willardi, S. catenatus, S. miliarius*) and combined with *C. atrox* data from Chapter 3. Isometry again was found for most variables intraspecifically, with measurements of the head (like those shown in the intraspecific analysis) commonly demonstrating negative allometry with respect to increasing body size. Using independent contrasts for interspecific comparisons, no regression slopes for morphological variables were found to be significantly different than regression slopes predicted by isometric growth. Morphological results again satisfied the assumptions of geometric similarity for predictions of the Hill (1950) model to be valid: maximum acceleration should decrease with increased size. Using identical filming protocols as those used in the intraspecific study, I collected values for kinematic strike variables for 13 adult snakes from five rattlesnake species (*C. lepidus, C. viridis, C. willardi, S. catenatus, S. miliarius*). These values were combined with values from five adult

C. atrox recorded during intraspecific analyses. Multiple strikes were recorded for all 18 snakes, with maximum performance values attained by a given snake over all of its recorded strikes being used in the analyses. Regression analysis of independent contrasts again revealed size-independence in maximum acceleration, in contrast to the kinematic predictions of Hill (1950).

Chapter 2

Kinematic comparisons between predatory and defensive strikes in the western diamondback rattlesnake (*Crotalus atrox*)

INTRODUCTION

The predatory strike of vipers (Viperidae) is a distinctive behavior in animals. In less than half a second, a snake lunges from a resting position, erects its elongated fangs, injects venom into its prey and returns to its original position, presumably to escape retaliation from its victim (Kardong, 1986a; Kardong and Bels, 1998). The elongated maxillary fangs rotate forward almost 90º during the strike (Cundall, 2002) and penetrate the prey, allowing primarily hemotoxic venom to be injected. The venom can subdue and predigest prey before ingestion, establishing an advantage to deep penetration of the fangs. Neuromuscular coordination must therefore be precise in the strike.

Defensive strikes, especially those of rattlesnakes (*Crotalus* and *Sistrurus*), often include a defensive display towards their attackers, particularly

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when the perceived threat is persistent and/or when the aggressor makes a sudden movement. Often the head of the snake is elevated between the body coils, and distinctive warning sounds are produced with the caudal rattle. These displays are typically followed by a rapid strike delivering an injurious and sub- or lethal-dose of venom upon fang contact.

Historically, predatory and defensive strikes in rattlesnakes were distinguished by a variety of qualitative pre-strike and strike behaviors. The snake rattles during defense (Minton, 1969; Klauber, 1972), the head is not flexed ventrally at contact with the target (Kardong, 1986b; Janoo and Gasc, 1992), and the strikes proceed from elevated, vertical S-coils (Duvall et al., 1985). Slow-arcing tongue flicks studied in various colubrid species (Gove, 1979; Gove and Burghardt, 1983) were also proposed as a character potentially delineating defense strikes in rattlesnakes (Hayes and Duvall, 1991). Comparisons between the two strike types were further confused by general descriptions of rattlesnake strike variables and behavior that clearly include defensive strike situations (Vigne, 1833; Mitchell, 1861; Coues and Yarrow, 1878; Van Riper, 1954; Lester, 1955; Klauber, 1972; Russell, 1980). Although recent literature includes studies of such predatory strike variables as timing, behavior, and venom metering (Hayes et al., 1992; Hayes, 1993, 1995; Hayes et al., 1995; Kardong, 1986a, b; Kardong et al., 1986; Kardong and Bels, 1998), no study to date details quantitative differences between predatory and defensive strikes.

Are predatory strikes faster than defensive strikes to overcome the optimal escape behavior of potential prey items? Do maximal velocity and acceleration of the rattlesnake head prevent potential prey from eluding strikes? Conversely, might defensive strikes be faster than predatory strikes because startling or confrontational situations require maximal velocity and acceleration to deter predatory attack? For the two strike types, this study quantitatively evaluates

velocity, acceleration, and timing variables of the rattlesnake head from the initial movement of the snake toward its target until the contact of jaws on the target.

MATERIALS AND METHODS

Four western diamond-backed rattlesnakes (*Crotalus atrox*), ranging from 58.0 to 92.5 cm total length, were collected from south-central Texas and used here. Animals were housed individually, kept on a 12L:12D light cycle and maintained over six months. Snakes were offered food (both live and dead laboratory mice) every two weeks and water was given ad libitum. Guidelines and safety features for the care of all rattlesnakes followed Gans and Taub (1964), Murphy and Armstrong (1978), and Altimari (1998), as well as guidelines established specifically for this study in conjunction with the University of Texas Animal Care and Welfare Committee.

The filming area consisted of a terrarium (L90 x W50 x H50 cm), bounded on three sides by glass and on the fourth by a sheet of pegboard with a small hole cut in the side; the floor was composed of white foam board. A 1-cm grid pattern traced onto film velum was placed onto the back glass pane to enable absolute distance measurements. A subject was placed unrestrained into a partitioned area (L50 x W50 x H50 cm) in the test arena 15–30 min before filming to allow for acclimatization. Two 15 W fluorescent bulbs were used to backlight the film velum placed on the back of the terrarium, and were left on during the acclimation period of each subject. The temperature during filming was kept at 27 ± 0.5°C.

Each predatory strike sequence was recorded with a Redlake MotionScope 1000S video camera at 1000 fps. A Canon ES970 8 mm video camcorder was

placed above the arena to quantify whether strikes were directed at 60º–120º to the optical axis of the high-speed camera with strikes exceeding this range being excluded. A single 250 W incandescent flood lamp was used to illuminate the terrarium 15–20 sec before introduction of prey items. A single, freshly-euthanized mouse was introduced on the end of 62 cm forceps through the pegboard hole 10–20 sec following removal of the terrarium partition. The euthanized mouse was moved slowly toward and away from the snake in a plane perpendicular to the camera's optical axis until the snake struck. All subjects showed intense interest in the prey item, often characterized by a series of rapid tongue flicks and at times pursuit of the mouse, resulting in an off camera strike.

Laboratory mice were used to elicit predatory behavior in the subjects because they were previously found to produce predatory behaviors in snakes equivalent to those elicited by wild rodent prey (*Peromyscus*; Kardong, 1993). Dead mice were used in place of live mice in order to remove potentially confounding and unrepeatable kinematic effects of live mice when struck. Prey mass varied between 4.0 and 14.5% of snake mass (mean = 7.02%). Hunger may heighten responsiveness to certain forms of stimuli (Hayes and Duvall, 1991; Hayes, 1993), so all snakes used in this portion of the analyses were offered laboratory mice (both live and dead) on a regular two-week basis.

Defensive strikes were filmed using the same camera configuration. Framing rate was reduced to 500 fps due to magnification constraints caused by the size of the defensive target (see below), with subsequent images blurred slightly. Because kingsnakes (genus *Lampropeltis*) are known to feed upon rattlesnakes, their visual or chemical presence would presumably enhance a defensive response, and in fact, rattlesnakes frequently strike kingsnakes during defensive encounters (Klauber, 1972). The desert kingsnake (*L. getula splendida*) is found sympatrically with *C. atrox* in south-central Texas. A small, stuffed,

yellow doll (100 mm tall, 70 mm wide, 26.5 g) was housed with an adult *L. getula* for 30–60 min before it was used as a defensive target, and was introduced to rattlesnakes on the end of 62 cm forceps through the side of the terrarium. Presentation of the doll was in an erratic and confrontational manner. The subjects likely interpreted this doll as a threat because of its large size, its odor (acquired from *L. getula*), and its behavior. Further, subjects rattled during every presentation of the doll and performed long arcing tongue flicks prior to each strike, which were only seen during presentation of the doll. No flawed strikes (e.g., collision with obstacle or side of cage prior to target contact, only one fang driven into target, snake missed the target entirely; Kardong, 1986b) were included in the analysis.

The strike of rattlesnakes was previously divided into four stages: extension, contact, release, and retraction (Kardong and Bels, 1998). The extension stage is defined as the period between initiation of forward movement to target contact, and the contact stage is the entire period of prey contact. The release stage begins upon freeing of jaw contact from the target and ends with jaw closure. Retraction involves the period of movement away from the target. Using these definitions, the release and retraction stages overlap greatly with each other, although each deals with a slightly different head/jaw movement. Variables presented in this analysis are measured mostly from the extension and contact stages, with a single variable (maximum gape angle, release stage) taken from the release stage.

Filmed sequences were downloaded to videotape and analyzed using a MiroMotion frame grabber (Pinnacle Systems GmbH) and the software programs Adobe Premiere 4.2 (Adobe Systems Inc.) and NIH Image 1.62 (developed at the U. S. National Institutes of Health and available on the Internet at http://rsb.info.nih.gov/nih-image/). Analysis of films began at the frame of

initiation of forward movement toward the target, and included the entire extension stage and up to 20–25 frames of the contact stage. Analysis of films ended at a maximum of five frames after secondary jaw contact, save calculation of maximum gape angle (release stage). Three distinct points on the snake head were used as landmarks (tip of snout, tip of lower jaw, angle of jaws [angle between jaws with the apex at the corner of the mouth]; Kardong and Bels, 1998). Maximum gape angle (MGA) was recorded for both the extension and release stages (Kardong and Bels, 1998). Distance from target was determined as the maximum straight-line distance between snake and target in the frame of initial movement toward the target. Time intervals, such as time to maximum gape angle (extension stage), time to contact of lower jaw with target, and time to contact of upper jaw (palatomaxillary complex) with target were also recorded. Percentage of the body kinematically active during the extension stage was obtained from the 8 mm video record. Duration of contact with target was initially recorded using the high-speed camera, but was not included in this study because many defensive strike sequences involved the snake moving both the target and itself off camera. Contact time could not be reliably estimated from the overhead (30 frames/sec) camera.

Velocities and accelerations were calculated using QuickSand.008 (Walker, 1997) using a smoothing algorithm (Kosarev-Pantos with odd extension algorithm) recommended by Walker (1998) for use with high-speed film. Cartesian coordinate data were analyzed separately in QuickSand.008, and were combined to yield velocities and accelerations; all acceleration values are absolute values. Instantaneous velocity is the distance traveled between frames divided by the time interval (predatory: 0.001 sec; defensive: 0.002 sec), and instantaneous acceleration is the change in velocity divided by the elapsed time. Velocity and acceleration values presented here are averages across the time intervals outlined

below (Wainwright et al., 1991). Average velocity (V_{avg}) and absolute average acceleration (A_{avg}) values were calculated for the periods of movement of the tip of the snout from the frame of initial forward movement to the frame of target contact with both jaws (extension stage plus initial portion of contact). Average velocity ($V_{contactavg}$) and absolute average acceleration ($A_{contactavg}$) values were also calculated for the time period between target contact of the first (often the lower) and second (usually the upper) snake jaw. Maximum velocity (V_{max}) and absolute maximum acceleration (A_{max}) values were determined for the each of these previous two time periods.

To address problems in measuring of velocity and acceleration from video data emphasized by Harper and Blake (1989a, b) and Walker (1998), a single predatory and a single defensive strike were each digitized 10 times by two individuals (Wainwright et al., 1991). Velocity and acceleration values were calculated for each of the 10 replicates. The coefficient of variation (CV) for V_{avg} was 1–6% for both data sets and both investigators. The CV for A_{avg} was 6–12% for both data sets and for both investigators. The CV's for V_{max} and A_{max} ranged from 2–4% and 13–20%, respectively, in the predatory strike and 10–30% and 30–40%, respectively, in the defensive strike. Measurement errors of displacement or velocity may increase with increased filming speed (Harper and Blake, 1989a, b; see also Walker, 1998), and V_{max} and A_{max} values may be underestimated. The CV's presented here indicate that my film analysis protocol provides an acceptable level of measurement error for average velocities and accelerations (Wainwright et al., 1991). Maximum instantaneous values for both variables, however, should be viewed as estimates, albeit comparable across individuals.

To test for kinematic differences between predatory and defensive strikes, 13 dependent variables were analyzed with a two-way ANOVA (factors of

individuals and strike type). A one-way ANOVA was used to test the effects of both snake size (SVL < 700 mm or SVL > 700 mm, two snakes in each group) and strike initiation distance (> 4 cm and < 4 cm) on kinematic variables (Kardong and Bels, 1998). Multiple comparisons between kinematic variables were also examined using Pearson correlations. Pairs correlated at $r > 0.5$ were examined further using linear regression analysis at $P < 0.05$ (Sokal and Rohlf, 1995). All statistical tests performed using StatView 5.0.1 (Abacus Concepts Inc.).

RESULTS

A total of 26 strikes (13 predatory and 13 defensive) were analyzed. Four predatory strikes were analyzed for one snake, and three for the other three snakes. Four defensive strikes were analyzed for one snake (not the same snake with four predatory strikes), and three analyzable defensive strikes were available for each of the remaining snakes. Representative video stills from a single snake for both a predatory and defensive strike sequence are presented in Figures 1 and 2. Representative values of velocity and acceleration for a single snake during each strike type (for the extension stage and first portion of the contact stage) are given in Figure 3.

Predatory Strike Kinematics

Predatory strikes were initiated at a variety of distances from the prey item (range 0.75–15 cm). Of the strikes in which both jaw contact times can be

determined (N = 12), the lower jaw contacted the prey item first in 11 times, and in a single strike both jaws contacted the prey item within the same millisecond. The entire extension stage lasted from 18 to 73 (mean = 49 msec), and the first jaw (typically the lower jaw) preceded contact of the second jaw (typically the palatomaxillary complex) on average by 9 msec (range 2–22 msec). On average, 28% of the rattlesnake's body was involved in the forward motion of the predatory strike (Table 1).

During the extension stage, maximum gape angle (MGA) typically occurred toward the latter portion of the stage, between 1–5 msec prior to contact in eight strikes (mean = 6 msec, N = 12 strikes). The MGA of the extension phase was always less than the MGA of the jaws during the retraction stage in predatory strikes (Table 1). All strikes included a release and retraction stage; prey was never held during predatory strikes.

Maximum velocity and absolute maximum acceleration occurred at or between initial and secondary contact of the target by the snake jaws in 10 of 12 strikes and in 12 of 12 strikes, respectively. In the two strikes in which maximum velocity was achieved prior to prey contact, maximum velocity was reached 5 msec before contact. As a result, $V_{contactavg}$ and $A_{contactavg}$ were higher than throughout the entire extension stage in the majority of predatory strikes.

Defensive Strike Kinematics

Defensive strikes were initiated at a range of distances comparable to those of predatory strikes (range 2–17 cm). The lower jaw contacted the target first in 10 of 13 strikes, preceding contact of the upper jaw on average by 8 msec (range 2–22 msec). The upper jaw (palatomaxillary complex) contacted the target first on a single defensive strike (preceding lower jaw by 4 msec), and both jaws

contacted the target within the same millisecond in two strikes. The entire extension stage lasted from 42 to 70 msec (mean = 50 msec).

During the extension stage, maximum gape angle (MGA) typically occurred toward the latter portion of the stage, between 1–5 msec prior to contact in seven strikes (mean = 5 msec, N = 13 strikes). The MGA of the extension phase again was always less than the MGA of the jaws during the retraction stage in defensive strikes (Table 1). All strikes included a release and retraction stage; prey was never held during defensive strikes. On average, 37% of the rattlesnake's body was involved in the forward motion of the defensive strike.

Maximum velocity and absolute maximum acceleration occurred at or between initial and secondary contact of the target by the snake jaws in four of 13 strikes and 10 of 13 strikes, respectively. In the nine strikes in which maximum velocity was achieved prior to target contact, V_{max} was reached 2 msec (1 frame) prior to contact in four strikes, 6 msec prior to contact in three strikes, 12 msec prior to contact in one strike, and 14 msec prior to contact in a single strike. Of the three strikes in which absolute maximum acceleration occurred prior to contact, A_{max} was reached at three different times (6, 20, and 36 msec).

Comparison of Predatory vs. Defensive Strike Parameters

The distance from the target at the point of strike initiation differs significantly between the two treatments as well as between individuals; defensive strikes were initiated at distances on average twice those of predatory strikes. Amount of the kinematically active body region also differed significantly between strike types, but not between individuals. However, time to initial contact and to secondary contact did not differ significantly either between strike types, or between individual rattlesnakes (Table 1). Time to MGA in the

extension stage was also not significantly different between predatory and defensive strikes or between individuals. Gape angles were not statistically significant between the two treatments, and only the MGA in the extension stage was significant between individuals (Table 1).

All three acceleration values differed significantly among individuals, but not between strike treatments. Significant differences occurred between strike types for V_{max} and V_{avg} (Table 1). Individual V_{max} values were also significantly different (Table 1). No significant difference occurred between strike types for $V_{contactavg}$. The highest overall V_{max} (5.5 m/sec) and absolute A_{max} (878 m/sec2) occurred during defensive strikes; peak V_{max} and absolute A_{max} values obtained in predatory strikes were 4.28 m/sec, and 824 m/sec2, respectively. No significant interactions occurred between strike type and individual for any variables, indicating effects of the two strike types were the same on all individuals for each variable (Table 1).

Effects of snake size and strike initiation distance on kinematic variables were analyzed using a one-way ANOVA. Snake size had a statistically significant effect for A_{avg} ($F_{1, 20} = 4.95$, $P < 0.04$), and strike initiation distance had a statistically significant effect for V_{max} ($F_{1, 20} = 6.31$, $P < 0.03$) and V_{avg} ($F_{1, 20} = 5.73$, $P < 0.03$). Pearson correlations between strike variables showed significant correlations ($P < 0.05$) between strike initiation distance and the three velocity variables, but strike initiation distance was correlated with no acceleration variable. Ten of the 15 pairwise correlations between the six velocity and acceleration variables were significantly correlated. Time to upper jaw contact was significantly correlated with time to lower jaw contact, time to MGA, and $V_{fastavg}$. Time to MGA was also significantly correlated to both time to lower jaw contact and $V_{fastavg}$, and the amount of kinematically active body region was significantly correlated with both strike initiation distance and V_{avg}.

DISCUSSION

The significant differences found between velocity variables of both predatory and defensive strikes reflect differences in the distance from the target upon commencement of the extension stage. Defensive strikes start from roughly twice as far away as predatory strikes. However, total time spent in the extension stage does not vary significantly between strike types or individuals, nor do any other timing variables differ between strike types or between individuals, consistent with the significantly higher velocity values seen in defensive strikes. Strike type does not have a significant effect on accelerations. Instead, acceleration values only vary significantly between individual rattlesnakes, indicating that there is no difference in acceleration between predatory and defensive strikes in *C. atrox*. Rattlesnakes reach higher velocities in defensive strikes by covering greater distances over which a constant acceleration, maximized regardless of strike type, is applied.

Six of the 13 variables show significant differences among individuals, including individuals initiating strikes at significantly different distances (Table 1). This variability in individual performance has been noted in timing and velocity calculations in the kinematics of prey capture in other vertebrate studies (Shaffer and Lauder, 1988; Wainwright et al., 1991), including rattlesnake feeding (Kardong and Bels, 1998). Sources of kinematic variation within a species could be potentially attributed to geographical, ecological, anatomical, and/or ontogenetic differences affecting any given individual, but statistical analyses of

these questions remain to be answered (e.g., ontogenetic effects related to size; T. LaDuc, unpublished).

Comparisons with Previous Kinematic Studies

Velocity and acceleration

High values of V_{max} and A_{max} indicate that a portion of the head is still moving quite rapidly after initial contact with target in predatory strikes (11 of 13 strikes). This contrasts with findings reported by Kardong and Bels (1998), who inferred that the head begins to decelerate just prior to target contact, perhaps in an effort to reduce jaw injuries from collision with the target. Although data for only a single point on the head are presented here, the data suggest that the snout reaches peak velocity and acceleration after primary contact of the lower jaw with the prey item.

The average V_{max} values for predatory strikes in this study (2.61 m/sec) are greater than average values for predatory strikes in other solenoglyphs, *Vipera ammodytes* (1.47 m/sec), and *Bitis gabonica* (1.55 m/sec) (Janoo and Gasc, 1992; for a review of colubroid strike speeds, see Cundall and Greene, 2000). The highest predatory V_{max} calculated for *C. atrox* (4.3 m/sec, this study) also exceeds the highest V_{max} reported by Janoo and Gasc (1992) for both *V. ammodytes* (2.2 m/sec) and *B. gabonica* (1.9 m/sec). Values of V_{max} and A_{max} in defensive strikes are reached prior to initial target contact in the majority (11 of 13) of strikes, consistent with findings reported by Kardong and Bels (1998) for predatory strikes. The head velocity of *Crotalus viridis* reported by Van Riper (1954) was between 1.6 and 3.5 m/sec during defensive strikes, comparable to the range found in *C. atrox* (2.5–5.0 m/sec; this study).

No acceleration strike data are available for other rattlesnake species or any other member of the Viperidae. Although absolute acceleration values (A_{max} and A_{avg}) do not differ between strike types, those of *C. atrox* are some of the highest recorded for vertebrates (see Van Riper, 1953, 1954; Grobecker and Pietsch, 1979; Bergert and Wainwright, 1997).

Gape angles

Maximum gape angles during the extension stage of the predatory strike are comparable to those presented by Kardong and Bels (1998) for *Crotalus v. oreganus* (85–90º), but are somewhat smaller than the maximum reported by Janoo and Gasc (1992) for *V. ammodytes* (108º). These values are likely equivalent to those presented for booid snakes (50–65º) by Cundall and Deufel (1999), who calculated the angle in a different manner (using the angle between the mandible and an axis parallel to the braincase at the quadrate-mandibular joint). Timing of the MGA just prior to initial jaw contact mirrors findings reported by Kardong (1975) for *Agkistrodon piscivorus.*

The slightly larger MGA seen in the extension stage of the defensive strike may be linked to the overall larger size of the stuffed animal target. Figure 2 illustrates the less frequent of two defensive strike behaviors seen in *C. atrox* with the strike directed at the doll's midbody. A majority of defensive strikes (11 of 13) were directed to the top of the doll's head and included a slight ventral flexion of the head after secondary contact (not pictured). Published figures of defensive strikes also illustrate a large MGA, up to 180º, especially at jaw contact (Van Riper, 1953, 1954; Lester, 1955; Russell, 1980; Kardong, 1986b). These figures, including Figure 2 of this study, also illustrate a potentially confounding factor in comparisons between the two strike types: targets used to elicit defensive strikes are often much larger than prey items. Many of these larger targets only offer a

completely, or nearly completely, flat, vertical surface for the rattlesnake to contact during its strike sequence, giving the strike an overall "stabbing" rather than "biting" appearance. A stabbing-type strike may be the direct result of a strike towards a large or awkwardly sized target (Dullemeijer, 1961). This difference in target size may additionally explain why behaviors seen in defensive strikes, such as a lack of dorsal neck arching, are seen when strikes are delivered to targets typically too large for the rattlesnake to consume.

A rapid withdrawal of its teeth by means of an exaggerated gape in the retraction stage leaves the snake better able to avoid potential retaliation by the target (Radcliffe et al., 1980; Kardong, 1986a; Kardong and Bels, 1998). Presentation of an even larger defensive target may further elucidate whether an increased MGA in the retraction stage is related to target size or strike type.

Timing of jaw contact

The sequence of jaw contact with the target for predatory strikes follows that previously described for other solenoglyphs (Kardong, 1975, 1986b; Janoo and Gasc, 1992, Kardong and Bels, 1998). The snake's mandibles make the initial contact with the prey item. Only once in the 13 predatory strikes did both upper and lower jaws arrive within 1 msec. Jaw contact sequences in defensive strikes also followed those described for predatory strikes, although both jaws arrive within the same 2 msec interval in three strikes, and the maxillary fang made contact before the mandible in a fourth strike. This last strike sequence may be a statistical outlier, caused by strike contact of the snout at the extreme concave angle of the doll's head. Cundall and Deufel (1999) found differences between strike initiation distance and different strike categories, but no significant difference was found in this study ($F_{1, 21} = 0.04$, $P > 0.84$), excluding the single defensive strike in which the maxillary fang contacts the target first.

Duration of extension

The extension stage of the strike (as defined by Kardong and Bels, 1998) does not differ in duration between predatory and defensive strikes (Table 1). The mean duration of the extend stage for strikes presented here (49.5 msec) is similar to that for *V. ammodytes* (45 msec) (Janoo and Gasc 1992), but considerably larger than that for large (SVL 528–683 mm) *Crotalus v. oreganus* (33 msec) (Kardong and Bels, 1998).

Kinematically active body region

Predatory strikes involved significantly less anterior body length than did defensive strikes (Table 1). Kardong and Bels (1998), who described a kinematically active anterior-third portion of the body and a static region during their analysis of predatory strikes, found similar predatory strike values for this kinematically active body region. Klauber (1972) estimated that rattlesnakes used over half of their body during defensive strikes, whereas Janoo and Gasc (1992) suggested that strikes of *Bitis nasicornis* that exhibited little head displacement represented defensive strikes. Data presented here do not substantiate either claim, because the kinematically active body region for defensive strikes was significantly greater than that for predatory strikes, but never exceeded 46% of the rattlesnake's total length. Before the advent of modern recording equipment, it is interesting to note that Mitchell (1861:21) was able to postulate that the rattlesnake "...is unable…to strike at a greater distance than one-half its length, while usually its projectile range does not exceed a third of its length." Coues and Yarrow (1878: 268) mentioned a mere 17 years later, "...it is as well to remember that the utmost range of a rattlesnake's blow is less than it's own length."

CONCLUSIONS AND IMPLICATIONS OF KINEMATIC DIFFERENCES

General descriptions of both predatory and defensive rattlesnake strikes are found throughout the literature, with many anecdotal descriptions perpetuating ideas and beliefs regarding comparisons of the two strike types. *Crotalus atrox* in this study initiated defensive strikes from distances twice those of predatory strikes, yet the extension stage (time from initiation of movement towards primary target contact) did not differ significantly between the strike types. Values of V_{max} and V_{avg} were significantly different between the two strike types, defensive strikes were ~ 1 m/sec faster than predatory strikes (both V_{max} and V_{avg}). Lack of significant differences between A_{max} and A_{avg} for both predatory and defensive strikes may indicate that absolute acceleration is maximized, no matter the behavioral context of the strike. The significant correlation of distance with the two velocity values, V_{max} and V_{avg}, identifies the dependence of velocity on strike initiation distance. Thus, the significant differences seen in the kinematics of these two strike types are caused by differences in strike initiation distance. By varying strike initiation distance, rattlesnakes interpret different targets based on size, individual experience, or ontogeny of rattlesnake body size. Additionally, shorter strike distances could improve fang placement whereas strikes from greater distances may reduce the chance of harmful interactions with aggressors: the precision of the predatory strike might not be needed when trying to deter would-be attackers.

A recent study by Young et al. (2001 [2002]) examined kinematic differences between predatory and defensive strikes in similarly sized (74–112 cm SVL) *Crotalus atrox*. Using filming techniques similar to those described in the

present study, Young et al. (2001 [2002]) found significant differences in strike distance and velocity between the two strike types, but determined values of maximum velocity and strike distance greater in predatory strikes than in defensive strikes, a result opposite to the findings reported in this study. Comparisons of predatory and defensive strikes between two different sets of rattlesnakes, as well as the treatment of every strike as an independent event (Young et al., 2001 [2002]), may underlie some of the differences between this and the present study.

Chapter 3

Effects of body size on the predatory strike of the western diamondback rattlesnake, *Crotalus atrox*

INTRODUCTION

Evolutionary and ontogenetic changes in animal body size are accompanied by compensatory changes in metabolism, shape, and locomotor pattern (Schmidt-Nielsen, 1984; Calder, 1996). Changes in body size can alternatively constrain or enable an animal by varying surface-to-volume ratios (such as heat loss and diffusion), access to food availability, and other functional and physiological relationships (Shine, 1991a). Kinematics (body movements exclusive of their underlying forces) are influenced by changes in size. Changes in body size due to maintenance of either geometric similarity (= isometry in shape) or kinematic similarity (i.e., a large movement being the scaled equivalent of a small movement, with time intervals being scaled equivalents as well; Alexander, 1985) may change the manner and method by which an animal moves. Comparative studies among animal species can identify general constraints imposed by body size by detailing interspecific differences in locomotion and metabolism. The study of feeding is no exception, but the majority of comparative studies on feeding in vertebrates have centered on interspecific comparisons between species of similar ecologies with similarly sized animals (Shaffer and Lauder, 1985; Reilly and Lauder, 1992). Descriptive papers on the

feeding in a single species of vertebrate typically focus on restricted size ranges of animals specifically to avoid ontogenetic-based variation (e.g., Young et al., 2001 [2002]). However, a number of studies, encompassing a wide diversity of lineages, previously examined the ontogeny of body size as it applies to feeding kinematics in vertebrates (cartilaginous fishes: Ferry-Graham, 1998; Robinson and Motta, 2002; bony fishes: Richard and Wainwright, 1995; Wainwright and Richard, 1995; Cook, 1996; Hernandez, 2000; salamanders: Hoff et al., 1985; Reilly, 1995; toads: O'Reilly et al., 1993; O'Reilly, 1998).

In making predictions on how size may affect animal kinematics, researchers frequently test their results against the theoretical predictions of Hill (1950), whose results on the behavior of whole muscles were extrapolated into a scaling model of whole animal dynamics. Hill's (1950) predictions of kinematic scaling were based on models of isometric (i.e., geometric) change in body size. The power function

$$Y=aX^{b} \quad (1)$$

can be used to describe relationships between variables that are related to size, where a is the scaling coefficient and b is the scaling exponent (Huxley, 1932; Alexander, 1985). Under a model of isometric growth, a linear measurement (l) of an animal's body is related to its mass (M_b),

$$l=aM_b^{1/3} \quad (2)$$

or conversely,

$$M_b=al^3 \quad (3)$$

Deviations from this model are termed allometric with exponents either greater (positive allometry) or less (negative allometry) than expected under isometry. For motion, as l and M_b increase under isometry, both timing variables and linear excursions are predicted to increase proportional to l^1 and $M_b^{0.33}$; velocity (v) is predicted to remain constant or proportional to both l^0 and M_b^0, but acceleration

(A) is predicted to decrease proportional to l^1 and $M_b^{-1/3}$. Numerous patterns in scaling of body size and feeding have been observed, including isometry of both morphology and function (O'Reilly et al., 1993; Ferry-Graham, 1998; O'Reilly, 1998), no change in feeding behavior over ontogeny (Hoff et al., 1985; Reilly, 1995), isometry in morphology and linear displacements with negative allometry in timing variables (Richard and Wainwright, 1995; Robinson and Motta, 2002), positive allometry in feeding morphology and both negative and positive allometry in feeding kinematics (Hernandez, 2000), and both isometry and allometry in both morphology and kinematics (Cook, 1996).

Snakes are an excellent taxon in which to investigate the effects of body size on feeding kinematics because of their substantial body size variation and a feeding system uncomplicated by limb movements. Many key morphological and behavioral innovations for feeding have arisen within snakes to complement their cylindrical and limbless bodies, such as the liberation of the mandibular symphysis, unilateral mandibular movements, and the use of venoms (Gans, 1961). The predatory strike of most venomous vipers (family Viperidae) is a behavior unlike any other in the animal kingdom. In less than half a second, a snake can lunge forward from a resting position, inject venom into its intended prey item via elongated fangs, and then return to its original position, presumably to escape the retaliatory effects of its victim (Kardong, 1986b; Kardong and Bels, 1998). The elongated maxillary fangs can rotate anteriorly more than 90° during the strike (Young et al., 2001 [2002]), and act as hypodermic needles injecting a primarily hemotoxic and proteolytic venom. Because the venom both subdues and predigests prey before ingestion, it is imperative that the fangs penetrate deep into the prey. The rotation of the fangs coupled with the rapid movement of the viper's head towards and then away from its (often mobile) prey is an exceptional demonstration of kinematic coordination. This feeding system also is different

from any previously-studied size-effect system because the feeding movements of the head are dependent on the extension of body segments; size-related effects in the snake feeding system are dependent not only on the size of the head but on the size of the recruited body segments that propel the head forward (and conversely, retract it) during a strike.

Rattlesnakes are members of the Viperidae clade and are found exclusively in the New World. These snakes display a large degree of intraspecific variation in body size, which, within some species, ranges over an order in magnitude (Klauber, 1937; Campbell and Lamar, 1989). Many previous descriptions and analyses of the strike behavior in rattlesnakes were restricted to prey preference (Chiszar and Radcliffe, 1977), amount of venom injected (Hayes et al., 1992; Hayes et al., 1995), and non-kinematic strike characteristics such as bite location (Minton, 1969; Schmidt et al., 1993), and post-strike behavior (prey release behavior: Kardong, 1986b; strike-induced chemosensory searching: Chiszar et al., 1986, 1992). The accessibility of high-quality video and high-speed film cameras over the last 40 years enhanced the kinematic analysis of 'fast system' (sensu Cundall and Greene, 2000) snake feeding activity (Frazzetta, 1966; Greenwald, 1974, 1978; Kardong et al., 1986; Janoo and Gasc, 1992; Kardong and Bels, 1998; Cundall and Deufel, 1999; Deufel and Cundall, 1999; Kley and Brainerd, 1999; Young et al., 2001 [2002]; Alfaro, 2002; Smith et al., 2002). Still, few papers have addressed ontogenetic effects on kinematic feeding variables within snakes. Results from these papers only demonstrated differences between two or three separate size classes and excluded specific discussions of body size changes or scaling of kinematic variables (Mushinsky et al., 1982; Kardong, 1986b; Hayes, 1991; Hayes et al., 1995; Kardong and Bels, 1998). A recent study on the Chinese pit viper (*Gloydius shedaoensis*) addressed body size

changes between two size classes (juvenile vs. adult, < 50 cm or > 50 cm, respectively) mainly with respect to diet and ambush sites (Shine et al., 2002).

The combination of the predatory strike of rattlesnakes and the ontogenetic range of body sizes within the clade present an opportunity to test whether changes in body size imposed constraints on the evolution of predatory strike performance. There are three ways to analyze strike variation: kinematics (motion), dynamics (force), and morphology; I will use both kinematic and morphological methods in this study. Three main questions will be investigated in this study: 1) what are body scaling relationships within a single rattlesnake species, 2) are these relationships accurate predictors of the scaling of strike kinematics, and 3) do strike performance parameters follow predicted models of kinematic scaling, based on either geometric or functional similarity?

The western diamondback rattlesnake, *Crotalus atrox*, was selected as the model system for examining body size effects on feeding in a terrestrial vertebrate for several reasons: accessibility (locally abundant in Texas), wide range of intraspecific body size (0.3-2.2 m: Klauber, 1937; Werler and Dixon, 2000), and recent kinematic work indicates suitability for allometry study (Kardong and Bels, 1998; LaDuc, 2002). Mass and length data available for *C. atrox* indicate positive allometry (Klauber, 1937, 1938). As individuals grow larger, body shape changes and snakes become much more heavy-bodied or stouter with age. Potential changes in shape and size may be evidenced in the kinematics of the predatory strike. Differences in kinematic variables may derive allometric scaling differences (seen previously in sounds produced by the rattle: Cook et al., 1994), or from actual structural reorganization of physiological components (e.g., reduction in volume and mass in the anterior third of the body). Because previous body dimensions were taken for only three linear measurements and values for both sexes were pooled (Klauber, 1937, 1938), body-scaling relationships within

C. atrox will be reexamined. By focusing on the overall length and mass of the animal, in addition to head size and body circumference, I can address those parameters integral to the strike: volume of the head and anterior half of the body, overall length and mass, and cross-sectional area (Moon and Candy, 1997). From these body-scaling relationships, I will predict scaling relationships in predatory strike parameters. If geometric similarity is maintained, I predict kinematic relationships to follow the predictions of Hill (1950). If animal growth is allometric, I expect functional or kinematic isometry in feeding variables (Sweet, 1980; Birch, 1999). Using acceleration (A) as a strike performance parameter, A under isometric growth would be proportional to either $M_b^{-1/3}$ or l^1 because

$$\text{force}(F) = M_b \times A \qquad (4)$$

and F is proportional to l^2 (i.e., cross-sectional muscle area proportional to L^2), and M_b is proportional to l^3, then

$$A = F / M_b \qquad (5)$$

which is proportional to either l^{-1} or $M_b^{-1/3}$. If acceleration scales in a corresponding isometric fashion, larger animals would require a relatively longer period of time to complete a strike than would smaller animals because the larger animals' muscle area could not account for the proportionally larger body mass. For larger rattlesnakes to demonstrate kinematic similarity relative to smaller snakes, the cross-sectional muscle area can not scale as predicted by geometric similarity (Sweet, 1980; LaBarbera, 1989). Assuming muscles are equivalent and the same relative mass of the snake moves during the strike, cross-sectional muscle area would need to scale with $M_b^{1.0}$ and not by $M_b^{2/3}$, the latter predicted by geometric similarity. Compilation of accelerational profiles for *C. atrox* individuals over a range of body sizes will address this question; additional variables taken from kinematic analyses may further support hypotheses of

scaling relationships suggested by body allometry. By quantifying both morphology and feeding kinematics, this study will integrate two levels of analysis into a broader picture of the predatory strike in rattlesnakes. Additional features, such as muscle motor patterns, then can be added to this analysis to further our understanding of this complex system.

MATERIALS AND METHODS

Morphological analyses

One hundred and twenty-six preserved rattlesnakes were examined from two university collections (see Appendix A). Specimens that were not obviously damaged or mutilated were measured and included in the analyses; some specimens that were damaged were used only for those non-affected variables. Linear measurements of snout-vent and tail length were taken to the nearest mm using lengths of string and a wooden meter stick. Linear measurements of the head were taken to the nearest 0.01 mm using digital calipers and included jaw length (distal tip of lower jaw to retroarticular process), head length (anterior of mental scale to transverse line connecting lateral retroarticular processes), width between eyes (at narrowest point), width between retroarticular processes on both mandibles, height of head at snout, height of head at eyes, and height of head at retroarticular process. Circumferences were measured to the nearest mm using a piece of string wrapped around the body at three different points: 1/4, 1/2 and 3/4 body length (pre-cloacal); cross-sectional area was then estimated using the formula $(((\text{circumference})/(2 \times 3.14))^2 \times 3.14)$ assuming body shape to be a circle.

Snake bodies are tubular (Cundall, 1987) or cylindrical (Greene, 1997), although cross-sectional outlines at 1/2 and 3/4 body length may be flattened along the ventral surface. Volumes of the head, anterior half of body and whole body were obtained via fluid displacement, with fluid measured in either a 10 or 50 ml graduated cylinder, with resolution to 0.1 and 1 ml respectively. Pre-existing, small ventral incisions in some specimens (if present, typically in posterior third of body) may have led to underestimates of total volume. Deviations in lengths and weights in the preserved specimens from live values were anticipated, but similar degrees of deviation were expected to be present in all specimens (Klauber, 1938: ~2% total length).

Video analyses

Kinematic and qualitative data were obtained from 20 western diamondback rattlesnakes (*Crotalus atrox*) collected from several counties in central and south-central Texas and were kept on the University of Texas at Austin campus. Snakes ranged in size from 345–945 mm total length, and 24–345 g in total mass. The size range of *C. atrox* used in this study represented age classes spanning from neonate to reproductively-active young adults (minimum snout-vent length [SVL] of reproductive female, 648 mm; Rosen and Goldberg, 2002). Snakes were collected over an 18-month period (March 1999 – October 2000), and were kept in a 12h: 12h, L:D cycle with warm (27-30 °C) air temperatures maintained year round. Each animal was housed individually in one of two different-sized glass aquaria measuring either 50 x 30 x 25 cm or 75 x 30 x 30 cm. Snakes were offered food (both live and dead laboratory mice) every two weeks, and water was given ad libitum. A small cardboard box in each cage served as a daytime refuge. Guidelines and safety features for the care of all

rattlesnakes followed Gans and Taub (1964), Murphy and Armstrong (1978), and Altimari (1998), as well as guidelines established specifically for this study in conjunction with the University of Texas Animal Care and Welfare Committee (Protocol #99031201). Most snakes were in captivity over four months before feeding trials and filming were initiated, a period of time previously found not to alter normal predatory behavior (Kardong, 1993; Alving and Kardong, 1994).

The filming arena consisted of an aquarium (90 x 50 x 50 cm), bounded on three-sides by glass and on the fourth by a sheet of pegboard with a small hole cut in the side; the floor was composed of white foam board. A 1-cm grid pattern traced onto film velum was placed onto the back glass pane to enable absolute distance measurements. The snake was placed unrestrained into a partitioned area (50 x 50 x 50 cm) in the test arena 15-30 minutes before filming to allow for acclimatization. Two 15 W fluorescent bulbs were used to backlight the film velum placed on the back of the aquarium, and were left on during the acclimatization period of each snake. A new sheet of 40-lb. brown kraft wrapping paper (Consolidated Plastics Company, Inc.) was secured to the bottom of the cage and was removed after each strike sequence was filmed. A dark 5 mm line was placed on each sheet of kraft paper as a reference for digitizing. Air temperature during filming was kept at 27±0.5°C.

Each strike sequence was recorded at 1000 fps with a Redlake MotionScope 1000S video camera. A Canon ES970 8mm video camcorder was placed above the arena to quantify whether strikes were directed at 60º-120º to the optical axis of the high-speed camera with strikes falling out of this range being excluded. Relative proportion of snake body length that was kinematically active during the strike also was obtained from this dorsally placed video camcorder. A single 250 W flood lamp was used to illuminate the aquarium 15-20 seconds before introduction of prey items. A single, freshly-euthanized mouse was

introduced on the end of 62 cm long forceps through the pegboard hole 10-20 seconds following removal of the aquarium partition. The euthanized mouse was moved slowly towards and away from the snake in a plane perpendicular to the camera's optical axis until the snake struck. All snakes used in this study showed intense interest in the prey item, often characterized by a series of rapid tongue flicks and at times, pursuit of the mouse, resulting in an off-camera strike.

Laboratory mice are known to produce predatory behaviors in snakes equivalent to those elicited by wild rodent prey (genus *Peromyscus*; Kardong, 1993). Dead mice were used in place of live mice in order to remove potentially confounding and unrepeatable responses created by mouse behavior prior to and during the strike. Prey item mass varied between 4.5–23.0% of snake mass (mean: 11.0%) to minimize undesired effects on strike behavior such as interpretation of prey item as a threat or holding onto prey item after the strike instead of a quick release (Radcliffe et al., 1980; Kardong, 1986b). Hunger may heighten responsiveness to certain forms of stimuli (Hayes and Duvall, 1991; Hayes, 1993), so all snakes used in this portion of the analyses were fed laboratory mice (both live and dead) on a regular two week basis, which included the regular filming schedule. Snakes were allowed to consume prey struck during filming. Snakes that did not strike during a filming session were not fed until the next filming event, regardless of whether the subsequent filming event was successful.

For each filming attempt, an individual snake was only allowed to strike at a single mouse and was filmed, at a minimum, once every 14 days. The interval between filming attempts was important because of modifications to subsequent venomous snake strike behaviors due to either previous energy (Lester, 1955) or venom expenditures (Livingstone, 1857:143; O'Connell et al., 1982; Kardong, 1986b; Hayes et al., 1992). Though venom replacement rates never have been

rigorously measured (for a review see Young et al., 2001 [2002]), estimated rates of venom replenishment range from 3–4 days (King, 1941) to two weeks (Oliver, 1944). The interval between filming attempts may also be important because of potential effects of previous strikes on the venom delivery apparatus (e.g., fang breakage: LaDuc, pers. obs.).

The rattlesnake strike was previously divided into four stages: extension, contact, release, and retraction (Kardong and Bels, 1998). The extension stage is defined as the period between initiation of forward movement to target contact, whereas the contact stage is the entire period of prey contact. The release stage begins upon freeing of jaw contact from the target and ends with jaw closure. Retraction involves the period of movement away from the target. Using these definitions, the release and retraction stages overlap greatly with each other, although each deals with a slightly different head/jaw movement. Kinematic variables presented in this analysis were taken from only the extension and contact stages.

Filmed sequences were downloaded to videotape and were analyzed using a MiroMotion frame grabber (Pinnacle Systems GmbH) and the software programs Adobe Premiere 4.2 (Adobe Systems Inc.) and NIH Image 1.62 (developed at the U.S. National Institutes of Health and available on the Internet at http://rsb.info.nih.gov/nih-image/). Analysis of films began at the frame of initiation of forward movement towards the target (including the entire extension stage), and ended at a maximum of five frames after secondary jaw contact. Three distinct points on the snake head were used as landmarks (tip of snout, tip of lower jaw, and mandible-quadrate articulation). Maximum gape angle (MGA) was estimated by measuring the angle between the mandible and a line parallel to the braincase extending through the mandible-quadrate articulation (Cundall and Greene, 2000). Strike distance was determined as the maximum linear distance

between snake (tip of snout) and prey in the frame of initial movement towards the target. Four time intervals (time to maximum gape angle, time to contact of mandible with target, and time to contact of upper jaw (palatomaxillary complex) with target, time interval between maximum gape and prey contact) were also recorded. Mean, minimum, and maximum times for each of the four timing variables were included in the analyses. Timing values to contact for maximum and minimum distance (= maximum and minimum distance from strike initiation to prey contact) and timing value to overall maximum gape were also included in the analyses.

Duration of contact with target was initially recorded using the high-speed camera, but was not included in this study because many strike sequences either involved the snake moving both the target and itself off camera, or because contact between snake mandibles and mouse could not be visually confirmed. Contact time could not be reliably estimated from the 8 mm (30 frames/second) camera. Percentage of the snake body that was kinematically active during the extension stage was estimated from the 8 mm video camera and was defined as the portion of body that moves towards prey item (including recruited body segments). Although this definition may overestimate the portion of the body muscles actually contracting during extension ('active' recruitment of body segments during a strike can only be verified via electromyography), estimates based on this definition were repeatable by multiple observers and were subject to less bias than other estimation definitions.

Velocities and accelerations of the snout were calculated from positional data using QuickSand.008 (Walker, 1997) with a smoothing algorithm (Kosarev-Pantos with odd extension algorithm) recommended by Walker (1998) for use with high-speed film. Maximum velocity and acceleration values then were calculated for each sequence; mean maximum velocity and acceleration values

also were calculated for each individual using the mean of maximum values obtained from all strikes from an individual snake. I calculated error rates involved in the estimation of velocity and acceleration from this video-data acquisition system (LaDuc, 2002). A single strike was digitized 10 times by two human observers (Wainwright et al., 1991) with velocity and acceleration values calculated for each of the 10 replicates. The average coefficient of variation (CV) for maximum velocity and maximum acceleration estimates ranged from 2–4% and 13–20%, respectively. Measurement errors of displacement or velocity may increase with increased filming speed (Harper and Blake, 1989a, b; see also Walker, 1998), and maximum velocity and maximum acceleration values thus may be underestimated. The CV's presented here indicate that our film analysis protocol provides an acceptable level of measurement error for average velocities and accelerations (Wainwright et al., 1991, Harper and Blake, 1989b). However, maximum instantaneous values for both variables should be viewed as estimates, albeit comparable across individuals.

Statistical analyses

Morphological scaling variables were log-transformed and linearly regressed against log SVL, log total volume, and log mass using ordinary least squares (OLS) regression. Log-transformed cranial scaling variables were also regressed against all other cranial variables. Reduced major axis (RMA) slopes were calculated from OLS slopes and correlation coefficients (RMA slope = OLS slope/OLS correlation coefficient; Ricker, 1973; Swartz and Biewener, 1992). Reduced major axis, not OLS, regressions were used to test for deviations from isometry because levels of error in both independent and dependent variables were equivalent (Ricker, 1973; McArdle, 1988, LaBarbera, 1989; Swartz and

Biewener, 1992). Either OLS or RMA regressions could be used if appreciable variation is expected in the independent variable, with RMA results being preferred over OLS if results differed between the regression models (McArdle, 1988). Reduced major axis regressions are considered more robust than OLS when comparing cases of allometric growth (Ricker, 1973). Differences from isometry were determined using modified test statistic from Clarke (1980: 442) with degrees of freedom (d.f., rounded to nearest whole integer) calculated using Equation 5.1 from Clarke (1980) with a modification from McArdle (1988: 2332 [$n = N$-2]) and $\alpha = 0.05$. A modified Student's *t*-test was used to test whether regression coefficients for morphological variables differed significantly between the sexes (Zar, 1984: equation 18.1). Because of the multiple comparisons using the same data set, sequential Bonferroni (Dunn-Sidák) tests were also performed on all modified *t* statistics to reduce potential Type I errors (Rice, 1989; Sokal and Rohlf, 1995). All statistical tests were done using either StatView 5.0.1 or from formulas manually entered into Microsoft Excel.

Ordinary least squares regression was used in calculating allometric relationships between log-transformed kinematic variables and log-transformed values of SVL and mass. Reduced major axis regression was not used in the kinematic analyses because the majority of the error in the data was in the dependent data (see previous section), and was considerably greater than one-third the error found in the independent data (~ <1%, data not shown) that is recommended as a threshold for use of RMA over OLS (McArdle, 1988). Additionally, comparison of RMA regression slopes for kinematic data with those slopes predicted by isometry is not possible for predicted isometric slopes greater than zero. Use of OLS regressions also facilitated comparisons with previous data sets. Calculated slopes from OLS regressions were tested against predicted isometric slopes using a *t*-test procedure from Zar (1984: equation 17.18). Again,

sequential Bonferroni (Dunn-Sidák) tests were performed on all *t*-statistics with multiple and simultaneous comparisons (Rice, 1989; Sokal and Rohlf, 1995).

Kinematic data were analyzed using two different data sets: a complete set with a value for the maximum, minimum, and mean from all 20 snakes and a reduced data set containing a value for each snake for which there were ≤ 3 analyzed strikes.

To investigate interindividual effects, strike variables were analyzed via one-way analysis of variance (ANOVA). Values of $P < 0.05$ were considered to be statistically significant (Sokal and Rohlf, 1995).

Models of isometry

For morphological analyses, maintenance of geometric similarity was the null model. Although arguments for size-associated change in shape to maintain functional similarity are duly noted (Sweet, 1980), geometric similarity was chosen as the null model because it requires no *a priori* biological assumptions (Emerson and Bramble, 1993). Maintenance of geometric similarity (i.e., isometry) was modeled in log-log plots by a slope of one between linear dimensions, a slope of two between a linear dimension and an area dimension, and a slope of three between a linear dimension and a volume (or mass assuming constant density) measurement. Calculated slopes larger than predicted isometric slopes would demonstrate a positive allometry and calculated slope deviations smaller than predicted slopes demonstrate negative allometry. For kinematic analyses, isometric predictions by Hill (1950) served as the null models. All kinematic variables were log-transformed and regressed against both log SVL and log mass.

RESULTS

Morphological analyses

Isometric growth was the predominant scaling pattern found in all variables save one, head volume (Tables 2 and 3, Figures 4-7). Head volume demonstrated negative allometry in both sexes when regressed against either SVL or mass. Two slopes (head volume vs. mass, both sexes) were significant after Bonferroni corrections. Of the raw data, only tail length and total weight were significantly different between the sexes (t = -5.528, $P < 0.0001$; t = -2.021, P = 0.045, respectively). No slopes were significantly different between the sexes after Bonferroni corrections.

Isometric growth was also the predominant pattern seen within the cranial measurements (Table 4, Figure 8) and when cranial measurements were regressed on either SVL or mass (Table 5). The majority of slopes were found to have slightly negative allometries, although none were significantly different from isometry after Bonferroni correction. For the raw data, three variables were significantly different between the sexes: quadrate width (t = -2.396, $P < 0.019$), eyes width (t = -2.594, $P < 0.012$), and eyes height (t = -2.334, $P < 0.023$). However, no slopes for cranial variables were significantly different between the sexes after Bonferroni corrections.

Kinematics

One hundred and three strikes from 20 western diamondback rattlesnakes were incorporated into the analyses. The numbers of strikes per individual varied from 1 to 11, with 16 individuals having three or more strikes. Mean velocity and acceleration values for the 103 strikes were 1.73 m/s and 169.72 m/s^2,

respectively. Sixty-one of the strikes were initiated from a distance ≤ 40 mm. Mean time to maximum gape for all 103 strikes was 50.8 ms with a mean interval of 4 ms between maximum gape and prey contact (see Tables 6 and 7 for complete list of character values and ranges). Maximum velocity and distance were significantly correlated with each other and with all timing and distance variables (all with $P < 0.02$); maximum velocity was not correlated with maximum acceleration or estimation of body proportion kinematically active (Table 8). Maximum acceleration was only significantly correlated to three timing variables: maximum gape, lower jaw contact, and upper jaw contact (all with $P \leq 0.003$).

Velocities and accelerations

Slopes for maximum velocity increased with increased size, but exhibited negative allometry in every comparison (Table 9, Figure 9) whether regressed against mass or SVL, with most slopes significantly different than zero (exception: maximum velocity vs. mass, reduced data set, $P = 0.11$). Mean maximum velocity also demonstrated negative allometry in all comparisons, with all slopes of mean maximum velocity being significantly different than zero. In the data sets regressed on mass, the slope for maximum velocity in the smaller data set was slightly less than the same regression in the larger data set. This decrease was the only exception, however; all other slopes for both maximum velocity and mean maximum velocity increased from the larger to smaller data set. Not all velocity slopes were significantly different from slopes predicted under geometric similarity, with only four regressions being statistically significant after the Bonferroni correction.

Both maximum acceleration and mean maximum acceleration scaled negatively with respect to rattlesnake size, although absolute regressions were

mainly positive (Table 9, Figure 10). None of the allometric coefficients were significantly different than zero. Regressions for maximum acceleration against mass were larger in the smaller data set, but this was the only example of a decrease in slope between the different-sized data sets. All of the slopes were larger than the expected slopes predicted by geometric similarity, but only half (four) of the acceleration-related slopes differed significantly after Bonferroni corrections.

Timing variables

The majority of the timing variables increased with increased rattlesnake size, but relative timing decreased with increased size (Table 10, Figures 11-13). The only exceptions to this were slopes for minimum interval gape to contact (all four comparisons), maximum time to upper jaw contact and maximum time to lower jaw contact (16 snake data set for both mass and SVL), maximum interval gape to contact (16 snake data set for SVL only), and time to contact-overall maximum distance (16 snake data set for mass only), for which the timing variable decreased with increased size. In all cases, no slope was significantly different than zero with the average correlation coefficient for all timing slopes being 0.077. With the large number of simultaneous comparisons (60), only seven regressions remained significantly different than the expected slopes predicted by geometric similarity after the Bonferroni correction.

Additional variables: strike distance and percentage of body involved in strike

Strike distances increased because both mass and SVL increased, with slopes for the three distance variables exhibiting positive allometry with respect to both mass and SVL (Table 11, Figures 11-15). A single exception was the minimum distance vs. SVL slope for the reduced data set that was significantly different from the geometric similarity slope before a Bonferroni correction.

Values of r^2 for strike distance variables in the reduced data set slopes were more than double those from the full data set in all but one case, with the single exception increasing by only 98%!

The percentage of the body kinematically active during the strike decreased because mass and SVL increased (Table 11). Both methods for calculating kinematically-active body portions showed the same relationships when regressed against mass and SVL, because all slopes were significantly different than the expected slopes in geometric similarity slopes, even with a Bonferroni correction. Although all body-proportion slopes were negative (indicating a decrease in active body proportions because size increases), none of these slopes were statistically different from zero (range of *P* from 0.068-0.735) and instead demonstrate mass independence.

Univariate comparisons: individuals

Variation among the 20 individuals was tested using a one-way ANOVA. Maximum velocity ($F = 3.866$, $P < 0.001$), maximum acceleration ($F = 2.066$, $P = 0.014$), and strike distance ($F = 1.854$, $P = 0.031$) were significantly different among the 20 snakes. Time to maximum gape ($F = 1.452$, $P = 0.128$), interval between maximum gape and prey contact ($F = 1.082$, $P = 0.386$), time to lower jaw contact ($F = 1.267$, $P = 0.230$) and time to upper jaw contact ($F = 1.507$, $P = 0.106$) were not significantly different among individuals. The percentage of body kinematically active during the strike ($F = 2.606$, $P = 0.028$) also was significantly different among individual snakes, but this variable was tested among only 18 individuals (two individuals with only single analyzed strike were removed).

DISCUSSION

Body scaling

The body of *Crotalus atrox* grows isometrically with the exception of head volume, which demonstrates negative allometry with respect to the rest of the body (Tables 2 and 3). Although the scaling exponents for head volume were not significantly different from predicted isometric values in all six comparisons after a Bonferroni correction, the regressions of head volume versus SVL and mass were the only regressions significantly different before this correction. Slopes for all seven dimensions of the head regressed against SVL or mass demonstrated negative allometry (Table 5), although again, no regressions were significantly different from isometry after a Bonferroni correction. The fact that both head volumes and linear cranial measurements were negatively allometric does suggest that overall head shape changes with increased size, and that juveniles have proportionally larger heads than adults. Similar results were presented by Klauber (1938) in an analysis of head dimensions within *C. atrox* (head length measured from rostral to posterior end of mandible at the retroarticular process): increases in head length were proportional to total length$^{0.662}$, with data for both sexes combined. Combining the values from this study for both sexes (no slopes were significantly different between the sexes for any morphological comparison) resulted in similar scaling exponents: increases in jaw length were proportional to total length$^{0.793}$ and increases in head length were proportional to total length$^{0.757}$. Low correlation coefficients for many of the cranial dimensions, especially those of head height, may be due to preservational effects. Head length was noted as generally being the only reliable head dimension for preserved specimens because “snake heads are so flexible and so

often distorted during preservation" (Shine, 1991b:107), and was thought to be more accurately measured than either head width or head depth (Klauber, 1938).

Information on the scaling of body growth in snakes is extremely limited, with studies reporting on head sizes in reference either to sexual dimorphism within a species or clade (e.g., Shine, 1991b, 1994), or to taxonomic or geographic variation (e.g., Nakamura and Smith, 1960; King, 1997), or to adaptations for the capture and ingestion prey (e.g.,Greene, 1983; Pough and Groves, 1983). *Vipera berus* (Old World Viperidae) have proportionally longer heads when snakes are shorter (Forsman and Lindell, 1993) and exhibit no sexual dimorphism in head size (Forsman, 1991). Based on a limited sample of 12 species, the family Viperidae was found to have cross-sectional muscle and skeletal area proportional to mass$^{0.66}$, similar to the relationship predicted by isometry (Moon and Candy, 1997).

Geometric similarity is the most frequently cited model of growth for head dimensions in previous feeding studies (e.g., Cook, 1996; Hernandez, 2000). Outside of the feeding literature, other studies identified strong departures from geometric similarity in cranial dimensions for genera previously thought to display isometric growth (Birch, 1999; McGown et al., 1999). For the toad *Bufo marinus*, most skull dimensions are found to be negatively allometric (Birch, 1999; positive allometry was only found for area of adductor foramen) suggesting that allometric shape change could be responsible for the maintenance of functional isometry in the skull if feeding in *B. marinus* were similar to that in other *Bufo* species (O'Reilly et al., 1993; O'Reilly, 1998).

Isometric scaling exponents for overall body morphology were not in agreement with previous findings of positive allometry in *Crotalus atrox* (Klauber 1937). Length-weight regressions from Klauber (1937) indicated body mass proportional to total length$^{3.3}$. The scaling exponent for data in this study for body

mass against SVL regression (sexes combined) was significantly different from the scaling exponent derived by Klauber (RMA slope 3.11, d.f. 84, $t = 3.12$, $P < 0.01$ using modified test statistic from Clarke, 1980). Two reasons may account for this discrepancy. First, Klauber (1937) measured freshly killed snakes, enabling him to collect weights and linear measurements before distortion by preservation. Total length was calculated to decrease by 2% in a series of snakes after preservation, and suggestions were offered that "for the highest accuracy" all material should be prepared the same way, whether they are freshly killed specimens or preserved specimens (Klauber, 1938:3). All specimens used in this analysis were preserved museum specimens so any bias inherent in using preserved material was assumed to be shared equally by all specimens. Second, snakes examined by Klauber encompassed a larger range of body lengths (0.26–1.68 m) than those preserved specimens examined for this study (0.24–1.10 m). Perhaps examination of a larger size range of snakes might have changed the allometric coefficients from isometry to positive allometry. Two lines of evidence support this latter contention. In the live snakes used for kinematic analyses (total length 345–945 cm), body mass was proportional to $SVL^{2.654}$. One set of 12 *C. adamanteus* (total length 0.46–1.69 m) were found to have body mass proportional to $SVL^{3.108}$ (Prange and Christman, 1976); measurements of another series of *C. adamanteus* (0.35–1.82 m) resulted in a similar scaling coefficient, with body mass proportional to $SVL^{3.16}$ (Klauber, 1937). Nevertheless, the preserved specimens examined herein covered the range of body sizes used in the kinematic analyses and support a model of isometric growth for all variables studied save those of the head.

One additional point of variation lies in the fact that this is a cross-sectional analysis (one observation per each of several individuals of different sizes), rather than a longitudinal analysis (more than one observation through time

per individual) morphological variation. Most previous analyses of snake morphology also were cross-sectional; few studies examined the morphology of snakes through longitudinal analyses, with variations due to snake age and year of sampling reported (e.g., Jayne and Bennett, 1990). I attempted to minimize the potential effects of geographic variation by using specimens collected from Texas localities, but studies of morphological variation across the distribution are unknown.

Kinematic scaling

In order to realistically test the kinematic predictions of Hill (1950), animal growth must be geometrically similar. Overall isometric growth in the body of *Crotalus atrox* satisfies this assumption. However, the kinematics of feeding did not follow all of the predictions of Hill (1950). Maximum acceleration was size-independent, with scaling coefficients (both maximum and mean maximum) not significantly different than zero, although most predicted slopes based on geometric growth were outside the standard error of the mean estimates for the calculated slopes. Maximum velocity demonstrated positive allometry and the two sets of variables (portion of body active during strike and timing variables) predicted to scale equally with increases in size instead scaled with negative allometry. Distance variables did not scale significantly different from predicted isometric slopes. Significant correlations were found between maximum velocity, distance and timing variables; maximum acceleration was not significantly correlated with distance.

Maximum acceleration was not previously tested in the context of intraspecific feeding allometry, but previous studies on various forms of intraspecific vertebrate locomotor allometry reported both mass independence and

positive allometry in scaling maximum acceleration to body size. In fish, the C-start type of fast-start locomotion is a burst escape response (Domenici and Blake, 1997; Hale, 1999), and can be comparable to the burst motion in the anterior half of a rattlesnake's body during a strike. Maximum accelerations in C-starts were size-independent in two fish species, *Salmo gairdneri* and *Pterophyllum eimekei* (Webb, 1976; Domenici and Blake, 1993), but body growth exhibited positive allometry. Body growth in the common carp, *Cyprinus carpio*, also demonstrated positive allometry, but maximum acceleration increased with increased size (proportional to mass$^{0.340}$) (Wakeling et al., 1999). For three species of frogs (*Bufo americanus*, *Pseudacris triseriata, Rana pipiens*) with isometric growth, acceleration in jumping was also size-independent (Emerson, 1978). A study of tail-flipping escape behavior in geometrically-similar lobsters demonstrated size-independence in average acceleration, which was partially attributed to the isometry shown in increased tail flip duration (Nauen and Shadwick, 1999). Maximum acceleration in rattlesnakes also was correlated with duration of the strike (initiation to contact of both jaws), but strike duration was not significantly different from isometry with respect to body size.

Maximum velocity frequently is estimated for scaling studies, especially of locomotion. In fish with positively allometric growth, maximum velocity was shown to scale with isometry with body length, (Webb, 1978), with negative allometry (Wakeling et al., 1999), and independent of body size (Domenici and Blake, 1993). Fish studies also showed that within a given distance, maximum velocity does not change over ontogeny (Webb, 1976; Dominci and Blake, 1993). Burst speeds were shown to increase with body size (positive allometry) within several lizard taxa (*Stellio stellio*, Huey and Hertz, 1982; *Leiolepis belliani*, Losos et al., 1989). Velocity was mass-independent in the escape response of the spiny lobster (Nauen and Shadwick, 1999). For snake strikes, maximum velocity

demonstrated with positive allometry, increasing, although not proportionally, with increases in body size. This finding does not support the kinematic predictions of geometric similarity by Hill (1950).

Timing variables were significantly correlated with maximum velocity (Table 8) because they, too, increased with increased body size, although with a negative allometry and markedly different slopes than the isometric slopes predicted by geometric similarity. In ontogenetic feeding studies, only the results of feeding in *Bufo* (O'Reilly et al., 1993; O'Reilly, 1998) support the timing predictions of Hill (1950); a single study on feeding in cottid fish found timing to demonstrate positive allometry, but it is unclear if this slope was significantly different than the isometric value (Cook, 1996). Work in salamander feeding revealed mass independence in timing variables (Hoff et al., 1985; Reilly, 1995). All other vertebrate feeding studies have indicated negative allometry in timing variables (Richard and Wainwright, 1995; Ferry-Graham, 1998; Hernandez, 2000, Robinson and Motta, 2002).

The repeated deviation of timing values slopes from predicted slopes for geometric similarity, even when geometric similarity characterized body dimensions (Richard and Wainwright, 1995; Ferry-Graham, 1998; Robinson and Motta, 2002; this study) suggests there may be potential explanations for the discrepancy: an ontogenetic change in underlying muscle motor patterns, muscle anatomy, and different scaling of muscle contraction rates. The feeding study on largemouth bass is the only study to date to integrate actual timing of muscle use along with morphology and other kinematic variables in an ontogenetic study of feeding (Wainwright and Richard, 1995; Richard and Wainwright, 1995). Kinematic results (such as deviations in timing from predicted slopes) could not be explained by ontogenetic shifts in muscle motor patterns because size had no effect on any feature of muscle activation such as onset and offset of firing, save

for a single adductor (Wainwright and Richard, 1995). One hypothesis of scaling for feeding timing variables (Richard and Wainwright, 1995: time proportional to length$^{0.33}$) was based on empirical data for scaling of muscle contraction rates in lizards, salamanders, and fish (Marsh, 1988; Bennett et al., 1989, Archer et al., 1990) rather than on the Hill (1950) prediction that force does not increase proportionally with increases in muscle mass. Empirical values for the scaling of time to peak isometric muscle tension to body length in three vertebrate species were 0.194 (Marsh, 1988: desert iguana, *Dipsosaurus dorsalis*), 0.29 (Archer et al., 1990: cod, *Gadus morhua*), and 0.465 (Bennett et al., 1989: tiger salamander, *Ambystoma tigrinum*). The average of these three values is 0.32, remarkably similar to the values for timing variables of Richard and Wainwright (1995), Ferry-Graham (1998), Hernandez (2000), Robinson and Motta (2002), and this study. In fact, the majority of rattlesnake strike timing variables were not significantly different from either length^{0} or length$^{0.32}$, but did differ from the predicted slopes based on geometric similarity from Hill (1950). Only the slope for minimum time interval between maximum gape and contact was significantly different [all four comparisons: both complete and reduced data sets against both body mass and snout-vent length]).

Strike distance was significantly correlated with changes in maximum velocity (Table 8). Distance scaled with positive allometry with increases in size in the rattlesnake strike, although not significantly different from slopes predicted by geometric similarity. This isometry is seen throughout other feeding studies with geometric growth.

Again, the kinematic analyses reported herein were based on cross-sectional, rather than longitudinal, samples. In the body-size feeding kinematic literature, longitudinal analyses were used once, in *Salamandra salamandra* (Reilly, 1995), where individual animals demonstrated kinematic similarity as

they grew between two defined size classes. Cross-sectional and longitudinal sampling produced generally similar results in studies of garter snake locomotion (Jayne and Bennett, 1990). This study attempted to minimize geographic variation by using snakes primarily collected from central Texas, but as with morphology, studies documenting geographic variation in kinematics are unknown.

Comparisons with other snake strike variables

Estimates of maximum strike velocity (3.63 m/s) and average maximum strike velocity (2.47 m/s, from the reduced data set) were comparable to the few published values for rattlesnakes (*C. atrox*: mean velocity, 3.31 m/s; maximum velocity, 3.46 m/s [Young et al., 2001 [2002]]; *C. viridis oreganus*: ~1.00 m/s [estimated by Young et al., 2001 [2002] from displacement graph in Kardong and Bels, 1998]; *C. v. viridis*: 2.47 m/s [Van Riper, 1954]). Velocities for other snakes included thamnophiine snakes (aquatic strikes for three species, 0.2 - 1.1 m/s, Alfaro, 2002), *Pituophis catenifer* (1.74 m/s, Greenwald, 1974), *Vipera ammodytes* (1.47 m/s, Janoo and Gasc, 1992), and *Pseudonaja textilis* (maximum velocity: 3.37 m/s, Whitaker et al., 2000). Similarities in these snake strike velocities may indicate limits to performance, especially because there was no difference in acceleration between predatory and defensive strikes in rattlesnakes (LaDuc, 2002). Two size classes of *Gloydius shedaoensis* were found to differ in average defensive strike velocities (0.74 m/s for juveniles [< 50 cm SVL] vs. 0.98 m/s for adults [> 50 cm SVL]), although slow video filming rates (25 frames/sec) and different average strike distances (8 cm for juveniles vs. 13 cm for adults) may account for the variation in velocity (Shine et al., 2002). Related to velocity measures in snakes, the ontogeny in snake sprint speed was found to scale with

positive allometry in *Thamnophis sirtalis* (Jayne and Bennett, 1990). Strike acceleration also was calculated in a single study for three species of garter snakes feeding on underwater prey (*Thamnophis couchii*, *T. rufipunctatus*, and *T. sirtalis*, 4.0 - 39.4 m/s^2, Alfaro, 2002).

Strike distances previously were reported previously for several non-venomous colubrid snakes (5-10 cm: Greenwald, 1974, 1978; 2.8-10.1 cm: Alfaro, 2002) and for predatory strikes of *Crotalus atrox* (6-7 cm: Young et al., 2001 [2002]). A notable exception to short distances was an Australian elapid (*Pseudonaja textilis*) whose mean defensive strike distance was 34 cm (Whitaker et al., 2000)! Two size classes of *Gloydius shedaoensis* (< 50 cm and > 50 cm) were shown to strike at different distances when presented with an identical defensive threat (Shine et al., 2002). Medium-sized *Crotalus v. oreganus* (46 - 58.5 cm) were shown to strike large prey items from further distances than small prey items (6.7 vs. 11.4 cm), whereas larger snakes (62 - 75.5 cm) struck both sized prey items from a single distance away from the prey item (12.6 cm) (Hayes et al., 1995). This result implies that rattlesnakes determine predatory strike distance, with prey size and perceived risk because obvious influences. Rattlesnakes also were able to choose different distances under predatory vs. defensive situations (Young et al., 2001 [2002]; LaDuc, 2002). If rattlesnakes are able to determine the distance to be traveled in a strike, if distance and velocity are strongly correlated (Table 8), and if velocity is dependent on intrinsic rates of muscle shortening, then changes in maximum velocity in this system are dependent on a minimum of two interrelated things: size of the snake and size of the prey item/target. Larger animals can choose a greater range of strike distances, whereas the intrinsic rate of muscle shortening scales to body $mass^{-0.33}$ (O'Reilly et al., 1995; Richard and Wainwright, 1995). Prey or target size influences the distance from which the snake will strike because there is a

minimum distance required to strike and to achieve envenomation and subsequent death or deterrence of target. Different-sized prey items and other targets have different levels of risk associated with this interaction (Young et al., 2001 [2002]). Risk likely decreases with increased snake size for many interactions. In the predatory strike of *C. atrox*, maximum velocity was not dependent on acceleration because no difference in maximum acceleration was found over a range of sizes and behavioral contexts (LaDuc, 2002; this study).

Interindividual variation

Variation between individuals is commonly seen in performance studies of animals, including feeding (e.g., Wilga and Motta, 1998; Wainwright and Shaw, 1999; Robinson and Motta, 2002) and locomotion (e.g., Garland, 1985; Losos, 1990; Bonine and Garland, 1999), although such variation may appear at times to blur trends in data (Robinson and Motta, 2002). Differences in performance values among individuals can be measured repeatedly and can be used in determining associations with other physiological and morphological characters (Bennett, 1987; Kolok, 1999). Most researchers dealing with feeding mechanics and size variation used multiple feeding sequences and maximum individual performance values in their studies of ontogenetic relationships (Richard and Wainwright, 1995; Hernandez, 2000; Robinson and Motta, 2002). Use of individual trials as independent events will likely mask repeatable individual variation and further cloud conclusions (Young et al., 2001 [2002]). Elimination of sub-maximally performing individuals was also recommended by Losos et al. (2002). For this study, three or more strikes were filmed and analyzed for 16 of the 20 snakes, with individual maximum values for velocity and acceleration used for scaling analyses. Partitioning the data into partial (values for all snakes with

three or more strikes, n = 16) and full (all 20 snakes) data sets revealed few major differences in scaling coefficients between data sets, although standard errors were reduced and correlation coefficients were increased (sometimes dramatically) in the smaller dataset (Table 9). In a previous study (Chapter 2), performance differences were found between individual snakes and strike types (predatory vs. defensive), such that individual rattlesnakes were consistent enough to possess recognizable and idiosyncratic strike kinematics; differences seen between individual snakes in this study can be attributed to variable animal size.

Implications of kinematic similarity

Functional similarity in the predatory strike was maintained throughout ontogeny of rattlesnakes despite isometric size change for most morphological characters. Negative allometry of head dimensions and mass independence in maximum strike acceleration are likely sources for the maintenance of kinematic function over ontogeny in rattlesnakes. Any advantages juvenile snakes can gain making them similar to adults may be important, because juvenile animals must deal with similar environmental pressures as adults, without the benefits of experience, locomotor agility ("effective and graceful locomotion"), and predatory ability (Carrier, 1996:478). Juveniles typically suffer from higher rates of mortality, particularly those in a locomotor transition stage, such as metamorphosing tadpoles (Wassersug and Sperry, 1977; Arnold and Wassersug, 1978). For a neonate rattlesnake, advantages of functional similiarity in maximum acceleration may help young snakes secure prey through their relatively larger heads and size-independent strike acceleration.

During a rattlesnake strike, the tips of the maxillary fangs diverge from one another as the maxillae are erected via movements of the palatomaxillary arch

(Mitchell, 1861). On average, fang tip spread in *Crotalus atrox* is 112% further apart at penetration than when at rest (Zamudio et al., 2000). This increase in the effective striking zone is thought to be advantageous to rattlesnakes (and to other vipers with similar skull architecture), particularly for large prey oriented perpendicular to the striking snake (Young et al., 2001 [2002]). During a strike, rattlesnakes may only successfully insert a single fang into a prey item either due to incorrect targeting by the snake or to detection and movement away from the rattlesnake by prey (Young et al., 2001 [2002]). Imperfect strikes such as these may represent up to 35% of all strike attempts, with reorientation and penetration of the unsuccessful fang occurring in almost half of these strikes, and usually within 100 ms of initial contact (Young et al., 2001 [2002]; LaDuc, unpub. data). Even in those strikes for which fang reorientation does not occur, venom injected from the correctly placed fang can, and generally does, subdue and kill the prey, although time to death may increase (Young et al., 2001 [2002]; LaDuc, unpub. data). The increased strike zone is thought to be disadvantageous in instances of prey oriented parallel to the strike trajectory, particularly for smaller prey items for which bilateral injection may be very difficult (Young et al., 2001 [2002]). An increased strike zone may be particularly advantageous to small snakes in most predatory situations. The relatively larger heads of youngsters gives them a slightly larger relative striking zone; this additional area may be crucial for opportunistic feeders like young rattlesnakes that must take advantage of every suitable meal they encounter. A single fang injected into a prey item establishes a contact point with the prey that may facilitate reorientation and penetration of the missed fang (Cundall, 2002). A failed strike can potentially represent a life-or-death situation for a neonate rattlesnake, particularly in late fall where only weeks have passed since birth and the active growing season is rapidly coming to an end (Rubio, 1998). Survivorship is lowest during the first few years of life because

young snakes often are food for various avian, mammalian, and ophidian predators (Fitch, 1949; Klauber, 1972; Greene, 1988; Brown, 1993, Bonnet et al., 1999). Survivorship increases with increased size (Parker and Plummer, 1987), so reaching an adult size as quickly as possible would be advantageous for a juvenile. Increased efficiency at acquiring food would help a snake reach that goal. If risk of death varies with age, then natural selection is expected to increase development through stages where mortality is highest (Williams, 1966).

Ontogenetic shifts occur in the diet and feeding behavior of colubrids (e.g., Mushinsky et al., 1982; Savitzky and Burghardt, 2000). Several water snake species (*Nerodia* spp.) change prey type as the snakes increase in length with corresponding modifications in predatory behavior for the different types of prey. Although the diets of certain rattlesnake species (e.g., *Sistrurus catenatus*, *C. lepidus*, and *C. willardi*) demonstrate marked shifts over ontogeny from invertebrates and lizards to mammals (Holycross and Mackessy, 2002; Holycross et al., 2002a,b), the diet of *Crotalus atrox* does not show a similar ontogenetic shift (C. Spencer, unpublished data). Absence of such a dietary shift does not explain the kinematic similarity found between neonate and young adult *C. atrox*, but animals feeding on the similar types of prey over their ontogeny might be expected to have comparable feeding kinematics and behaviors. This is the first study to document the feeding kinematics over the ontogeny of a rattlesnake species; no comparative intraspecific kinematic studies are available for rattlesnake taxa with pronounced dietary shifts, only brief behavioral observations were reported for young snakes feeding on 'unique' prey (centipedes: Rubio, 1998; H. McCrystal, personal communication).

Are there functional tradeoffs in the strike of *C. atrox* over their ontogeny to achieve kinematic similarity? Juvenile jackrabbits were found to accelerate more rapidly than adults, yet this specialization comes at the cost of reduced

maximum running speed and stamina (Carrier, 1995). Muscle metabolic capacities in juvenile stickleback fish show positive allometry, but this trend does not continue in adults, in which metabolic capacities are lowered to support reproduction (Garenc et al., 1999). Do corresponding tradeoffs occur in diamondback rattlesnakes? Nothing is known about the strike kinematics of neonate rattlesnakes, save the results of this study. Clumsiness and awkwardness of young animals previously was noted anecdotally (Carrier, 1995); perhaps there is a transition period of coordination between a neonate rattlesnake's relatively large head and its narrow anterior third of the body. Nothing is known about the ability of neonate rattlesnakes to meter their venom, and metabolic costs of venom production are not yet known either. Venom metering was demonstrated for different sized rattlesnakes for different sized prey (Hayes, 1991, 1993; Hayes et al., 1992, 1995) and for similarly sized rattlesnakes in different behavioral contexts (Young et al., 2001 [2002]). Integration of these studies along with kinematic results from this study could address effects of neonate strike performance on survival.

Integration of muscle activity patterns and architecture

Are underlying changes in the architecture and activation patterns of the axial musculature responsible for maintenance of kinematic similarity in the strike of *C. atrox*? Descriptions of snake axial musculature, including rattlesnakes (*C. horridus*: Tyson, 1682; *C. horridus* and *S. catenatus*: Mosauer, 1935; *C. adamanteus* and *C. cerastes*: Jayne, 1982), demonstrated that both epaxial and hypaxial musculature are bilaterally symmetrical and arranged as serial homologues throughout the length of the body (Mosauer, 1935; Gasc, 1981). Epaxial muscles typically span a greater number of vertebral or rib elements (6 -

35 in colubroid snakes: Jayne, 1982) than hypaxial muscles (usually spanning only a single segment: Mosauer, 1935; Auffenberg, 1962), and were hypothesized to be the muscles primarily responsible for lateral bending of the body (Mosauer, 1935; Gans, 1962). Organization of the epaxial musculature is highly complex with large amounts of interspecific variation present in muscular interconnection arrangements and vertebral insertion lengths for individual muscles (Gasc, 1981; Jayne, 1982). Specific examinations at only two or three points along the trunk revealed intraspecific as well as intracolumnar differences in the axial musculature (Pregill, 1977; Jayne, 1982). Ontogenetic variation in trunk musculature has not been assessed to date.

Kinematics of snake locomotion were described for a variety of taxa for a variety of locomotor methods (e.g., Mosauer, 1932; Gray and Lissman, 1950; Gans, 1962; Jayne, 1986; Moon and Gans, 1998). Although describing a majority of the locomotor methods present in snakes (sidewinding, lateral undulation, and concertina), only a few studies have described muscle activation patterns in snake locomotion, primarily focusing on the largest of the epaxial muscles, the semispinalis-spinalis, longissimus dorsi and iliocostalis (Jayne, 1988a,b; Gasc et al., 1989; Moon and Gans, 1998). Additional studies detailed trunk muscle recruitment patterns in swallowing and constriction (Moon, 2000a,b), but actual recruitment patterns have not been investigated for any strike behavior (predatory or defensive). Rattlesnake feeding strikes previously were modeled as either 'gate' (simultaneous or sequential straightening of anterior body curves) or 'tractor-tread' (anterior body thrust forward around a single postural curve) patterns (Kardong and Bels, 1998). The snake strike was hypothesized to be derived from concertina locomotion (Greene, 1997), believed to be the primitive locomotor mode in snakes (Gans, 1986) and similar to the gate model of Kardong and Bels (1998). Different regions of the body may be specialized for specific

behaviors, such as swallowing (Moon, 2000b) or striking. Structural or neural modifications to the axial musculature may be responsible for these specializations, but analyses of entire trunk activation patterns or muscle morphology (changes in muscle fiber to tendon ratios or modifications at the fiber type level) are absent as are studies relating to the ontogeny in axial muscles or muscle activation patterns. Energetic output-per-unit mass relationships could be altered with the recruitment of additional muscle fibers over increases in snake size as was suggested in the intraspecific mass-independence of mass in jumping frogs (Emerson, 1978). Future analyses of snake strikes conducted at the level of muscle activity and physiology should examine the simultaneous coordination of both postural muscle activities (elevation of head and anterior trunk) from muscle activity involved in forward acceleration of the trunk. Determination of relative percentages of different muscle fiber types (tonic vs. twitch) found within different regions of the epaxial musculature may additionally aid in the quantification of fundamental functional units in the trunk musculature of snakes (Guthe, 1981).

Definitive comparisons between results of this data set and previous feeding literature are difficult because of the diverse sampling of vertebrate lineages and ecologies, as well as feeding mechanics. Hydrodynamic concerns like low Reynolds numbers further complicate comparisons between larval fish feeding, adult fish feeding (much higher Re), and terrestrial frogs and rattlesnakes, although fluid-dynamic forces (such as drag) scale as a function of body size and are proportional to the density of the medium (830 times greater in water than in air) (Denny 1993; Richard and Wainwright, 1995). Feeding movements of the jaw and head from earlier studies alone are also difficult to compare to the coordinated and interdependent head and body motion found in the rattlesnake strike. Additionally, whether animal growth itself scales with

geometric similarity or allometry can severely restrict informative comparisons. However, the scaling similarities seen in several kinematic variables through the different vertebrate groups, whether they were a metric of locomotor or feeding performance, indicate that there may be underlying physiological and morphological reasons we can use to explain kinematic variation (i.e., differential muscle fiber recruitment; Emerson, 1978).

Chapter 4

A cladistic analysis of the rattlesnakes: a combined approach using both morphological and molecular data

INTRODUCTION

Rattlesnakes, with conspicuous rattles at the end of their tails, are one of the most identifiable ophidian groups found in the New World. There are over 30 species of these venomous snakes distributed throughout different habitats across the Americas, where they are found from southern Canada to northern Argentina. Because of both their venomous nature and their morphological distinctiveness, rattlesnakes were primarily the focus of immunological and taxonomic studies through the first half of the 1900's. More recently, rattlesnakes are being used as model systems in a variety of research programs, including muscle physiology, biomechanics, and behavior and natural ecology (see Beaupre and Duvall, 1998 for review of recent literature).

Rattlesnake systematics is of particular interest to many researchers because comparative studies between species often use phylogenetic estimates of relationships in order to account for bias in performance values or measurements due to historical relatedness (Harvey and Pagel, 1991). Few published phylogenies are available for species-level relationships within the rattlesnakes, however, a recent cladistic analysis of DNA sequence data (Murphy et al., 2002) was the first species-level phylogeny produced for rattlesnakes based on sequence

data. Some of the earliest published phylogenies are based on morphological and venom similarities, but do not include lists of characters used (Amaral, 1929; Githens and George, 1931). Of those phylogenies that discuss character analysis, neither character values of each individual taxon or descriptions of phylogenetic methodology are not included (Klauber, 1930, 1956, 1972; Gloyd, 1940; Smith, 1946; Brattstrom, 1964), making the results difficult to evaluate. To be fair, however, publication of these types of data were not commonplace at that time and explicit phylogenetic methodologies had not yet been theorized or elucidated. Compounding these evaluation problems, several of these phylogenies were not comprehensive in their coverage of rattlesnake species (Klauber, 1930; Smith, 1946).

The first exhaustive analyses of rattlesnake relationships were based primarily upon morphology. The relationships proposed by Gloyd (1940) were based upon similarities in structure, color pattern, and geographic distribution. Gloyd divided rattlesnakes into five distinct species groups (*C. atrox, C. durissus, C. triseriatus, C. viridis,* and *Sistrurus*) with six additional species having unknown affinities to any of his groups (*C. cerastes, C. enyo, C. polystictus, C. stejnegeri, C. tigris,* and *C. willardi*). Additionally, Gloyd only described relationships within species groups, and did not discuss relationships between species groups.

The phylogeny of Klauber (1956) was the first to explicitly outline species-group intra- and inter-rattlesnake relationships (Figure 16). Based on statistical and morphological data, this phylogeny maintained the five separate species groups of Gloyd (1940) with only one species (*C. stejnegeri*) outside species group boundaries. Three small modifications to this phylogeny were later presented by Klauber (1972): one species moved from one species group to another, one subspecies elevated to species-level, and newly described species

incorporated into the analysis. Neither of these phylogenies, however, was accompanied by character lists or weighting schemes used in the estimation of each phylogenetic hypothesis.

Cranial osteology was predominantly used by Brattstrom (1964) to create his hypothesis of pitviper relationships. Brattstrom provided illustrations and lists of character states for most of the individual cranial elements for each of the 57 taxa in his analysis, including 26 species of rattlesnakes. His phylogeny maintained the five species groups of Gloyd (1940), and like Klauber (1956), Brattstrom illustrated the relationships both between species and species groups. Only two species (*C. stejnegeri* and *C. polystictus*) were not placed into one of the five species groups. As with the previous phylogenies, no character list used to estimate the phylogeny was provided by Brattstrom ("Data concerning venoms, hemipenes, scutellation, etc., have been used when available," 1964:219).

Characteristics and components of rattlesnake venoms alone have been used to infer both generic-level relationships (Minton, 1956) and interspecific relationships (Leviton et al., 1964). These venom studies culminated with the phylogeny of Foote and MacMahon (1977) based on similarity values compiled from electrophoretic protein banding patterns. Although the characters and methodology used to create the phylogeny were categorically presented, the use of presence/absence of protein band data in systematic studies may invoke problems of character nonindependence (Buth, 1984). Additionally, workers as early as Gloyd (1940:15) recognized "venoms may be highly adaptive, since their primary function is that of procuring food," and that other characters might be better indicators of phylogenetic relationships rather than venom components and toxicities which may reflect environmental adaptations.

Two dorsal scale microdermatoglyphic characters were used to construct a rattlesnake phylogeny by Stille (1987:98), based on the premise that scale

microdermatoglyphic patterns “may reflect phylogenetic relationships rather than environmental adaptations” and could be informative at the familial or subfamilial level (Price, 1982). Characters and methodology used to create the phylogeny were explicitly stated, but data presented by Stille raises questions about the utility of potentially homoplastic characters with character states found in a variety of squamate families and genera being used to elucidate species-level relationships. Subsequent authors have similarly discounted this phylogeny based on the “known variability” of the two scale traits involved (e.g., Knight et al., 1993:364).

Estimates of rattlesnake relationships based on molecular evidence (not venom proteins) first appeared via comparisons of karyotypes (Monroe, 1962; Baker et al., 1972; Zimmerman and Kilpatrick, 1973) and blood serum proteins (Cohen, 1954, 1955). The distinctiveness of both *Crotalus* and *Sistrurus* (no *S. ravus* comparisons yet made) was supported in all comparisons, although no explicit phylogenies were presented because few taxa were examined. Several hypotheses supported *Sistrurus* as the basal member of the rattlesnake clade. Molecular evidence in the form of DNA sequence data was used to hypothesize species-level relationships only within the past 10 years (Knight et al., 1993; Parkinson, 1999; Murphy et al., 2002; Parkinson et al., 2002). Three of the four studies included only seven or eight rattlesnake taxa (including all members of *Sistrurus*: *S. catenatus*, *S. miliarius*, and *S. ravus*). The phylogeny of Murphy et al. (2002; mentioned above) was the first exhaustive species-level molecular analysis completed for the rattlesnakes; the remaining three studies addressed the monophyly of *Crotalus* and *Sistrurus*. The conclusions of Knight et al. (1993), based on sequence data for eight taxa from a portion of mitochondrial ribosomal DNA, supported monophyly for both genera, despite the most-parsimonious tree (depicting *Sistrurus* as monophyletic, with *ravus* nested in a paraphyletic

Crotalus) being rejected by those authors because it conflicted with existing morphological evidence. The phylogenies of Parkinson (1999) and Parkinson et al. (2002) included sequence data from multiple mitochondrial DNA genes for 57 pitviper species (seven of which were rattlesnakes) yet were unable to resolve the species-level relationships within the rattlesnakes with the small number of taxa included in these studies.

Although rattlesnake monophyly was never in question due to the complexity of the rattle (Zimmermann and Pope, 1948; Klauber, 1972) (all molecular analyses support monophyly as well), the relationship between, and memberships of, the two genera of rattlesnakes is under continual debate. Membership within *Sistrurus* differs between phylogenies with the exclusion or inclusion of *S. ravus*. Almost all morphology-based phylogenies place *S. ravus* within *Sistrurus* (the phylogeny proposed by Stille [1987] separated *S. miliarius* from *S. catenatus* and *S. ravus*), as do some molecular-based phylogenies (e.g., Knight et al.; 1993; some phylogenetic estimates from Parkinson, 1999 and Parkinson et al., 2002). Most morphological estimates confirm *Sistrurus* and *Crotalus* as sister taxa. However, several sequence-based estimates placed a monophyletic *Sistrurus* (including *S. ravus*) within a paraphyletic *Crotalus* (e.g., Parkinson, 1999). Other molecular estimates split *Sistrurus* and placed *S. miliarius* and *S. catenatus* as the sister group to *Crotalus*, with *S. ravus* as the basal member of *Crotalus* (Murphy et al., [2002]; some trees from Parkinson, [1999] and Parkinson et al., [2002]). The sister-relationship of *S. catenatus* and *S. miliarius* was generally supported in all estimates. Primitive (pleisomorphic) morphological characteristics found in *Sistrurus* (e.g., nine enlarged dorsal head scales, the lack of a transition between spines and ridges on the hemipenes, and a relatively longer, thinner tail) were used to separate the two genera. However, no morphological characters are yet identified as synapomorphies for the genus

Sistrurus; Brattstrom (1964) considered *Sistrurus* a subgenus of *Crotalus* based in part on this lack of distinguishing characteristics.

Despite the fact that the majority of large-scale (generic-level) analyses of viper systematics are based primarily on sequence data, a handful of studies incorporated both molecular and morphological evidence at this taxonomic level (e. g., Hermann and Joger, 1997; Gutberlet, 1998a; Herrmann et al., 1999; Werman, 1999). The use of morphology, for the most part, has been relegated to examinations of smaller sections of the family Viperidae (e. g., Gutberlet, 1998b; Branch, 1999), although even small partitions of the family are being examined with molecular techniques, including intraspecific analyses within the rattlesnakes (Pook et al., 2000; Ashton and de Queiroz, 2001; Douglas et al., 2002; Wüster et al., 2002).

So why have there been no broad-scale analyses of the rattlesnakes based on morphology since Klauber and Brattstrom? No cladistically-based or repeatable hypothesis exists for rattlesnake relationships based on morphology, yet older morphology-based hypotheses still serve as standards against which molecular data are interpreted (i.e., Knight et al., 1993; Murphy et al., 2002). Scutellation data were collected (Klauber, 1972), but the continuous nature of the data likely kept them from being included in phylogenetic analyses. Early authors, such as Brattstrom (1964) stated, "osteological characters are generally regarded as the most basic or least changeable and hence as more likely to indicate relationships than are features of the external morphology traits." In spite of this conception, a rigorous evaluation of rattlesnake osteology was never performed. The highly modified and kinetic skull of the rattlesnakes, along with strikingly similar body plans (Chapters 2 and 3), may have proved tedious and time-consuming to researchers trying to find suites of characters suitable for systematic analyses. Methods now exist that permit incorporation of previously

excluded and potentially informative variation and polymorphisms. Even the identification of phylogenetically uninformative apomorphic characters can be invaluable to other researchers, such as paleontologists who are restricted to variations in osteology to identify taxa. Conversely, discovery of osteological synapomorphies disclosure of intraspecific variation would afford paleontologists more confidence in their diagnoses, even if such diagnoses were made at higher and less specific taxonomic levels.

Rattlesnakes are a tractable group on which to focus systematic efforts using a combined approach. Molecular data exist for four genes (ND5, 12S, $tRNA^{val}$, 16S), some 2300 bp, for the majority of rattlesnake taxa. Information on scutellation and soft anatomical characters exist in the literature (Klauber, 1972) as do values for osteological characters (Brattstrom, 1964). However, much of this latter set of values is difficult to reproduce because of vague or generalized character state definitions. The availability of museum skeletal specimens for all but two taxa allows for a rigorous examination of osteological variation and phylogenetically informative characters. A combination of available morphological and molecular data will combine evidence to find the best tree (Kluge, 1989). With a robust estimate of rattlesnake relationships derived from two sources of data, many evolutionary and comparative questions previously untestable outside of a phylogenetic framework can now be addressed, ranging from biomechanical (Chapter 5) and physiological questions to broad systematic issues.

In this chapter, I combined previously reported data for scalation and hemipenial characters (Klauber, 1972), molecular sequence data available from GenBank (Murphy et al., 2002), and osteological data collected from skeletal specimens to create a data set of more than 2300 characters. I chose not to include characters related to pattern and coloration because of the recognized

effects of local adaptation (Brattstrom, 1964; Klauber, 1972; personal observations), in spite of recommendations to the contrary by Amaral (1929) and Gloyd (1940). I then compared this phylogeny to previously published hypotheses of rattlesnake relationships using non-parametric tests (Templeton, 1983). Comparisons are made to species-level relationships suggested in the literature as well as to the hypothesized relationships between, and memberships of, the two rattlesnake genera, *Crotalus* and *Sistrurus*. This study is the first to combine both morphological and molecular data to estimate species-level rattlesnake relationships.

MATERIALS AND METHODS

Phylogenetic analyses incorporated morphological (mensural, meristic, hemipenial, and osteological) and molecular data from most recognized species of rattlesnakes (Appendices A and B; McDiarmid et al., 1999). Exceptions to this taxonomic sampling are those six taxa recently elevated to species status within the *Crotalus viridis* complex (Douglas et al., 2002: *C. v. abyssus*, *C. v. cerberus*, *C. v. concolor*, *C. v. helleri*, *C. v. lutosus*, and *C. v. oreganus*), four taxa from the Gulf of California recently elevated to species status (Grismer, 1999: *C. mitchellii angelensis*, *C. m. muertensis*, *C. molossus estebanensis*, and *C. ruber lorenzoensis*), and *Crotalus lannomi*, known only from the roadkill holotype. *Crotalus unicolor* and *C. vegrandis* were treated previously as either full species (Gloyd, 1940; Klauber, 1972; Murphy et al., 2002) or as subspecies of *C. durissus* (Campbell and Lamar, 1989). Data for 15 mensural, meristic, and hemipenial

characters were taken from published references (Appendix D; Klauber, 1972; McCranie, 1988). Data for 192 cranial osteological characters (Appendix D) were derived from 177 skeletal specimens of 30 rattlesnake taxa (see Appendix B). Some characters were taken or modified from Brattstrom (1964) or Gutberlet (1998a, b) and are indicated as such in Appendix D; the majority of characters are newly described herein and were elucidated from an initial subset of specimens using one specimen per taxon. Terminology for cranial osteology follows Baird (1960), Brattstrom (1964), Underwood (1967), Kamal and Hammouda (1965), Klauber (1972), Kardong (1973, 1990), Rieppel (1977, 1979), Bellairs and Kamal (1981), Savitzky (1992), and Kluge (1993). Osteological specimens of *Crotalus intermedius* and *C. transversus* do not exist and data for tooth counts in *C. intermedius* were taken from the literature (Smith, 1946). Characters and character states were initially identified and defined from the variation found using single disarticulated specimens from 20 different ingroup taxa (three outgroup taxa also were used in this initial analysis); minor descriptive modifications were made throughout the examination of the entire specimen group. Five articulated and five disarticulated adult specimens, when available, were examined for each taxon. Character states for each taxon were taken from disarticulated specimens for most characters; six characters could be scored only from articulated specimens. If five disarticulated specimens were not available for a given taxon, character states were taken from articulated specimens, though fully articulated skulls precluded elucidation of all character states for a given specimen (e.g., character 166: relative size of medial aperture of recessus scalae tympani – only visible in disarticulated otooccipital).

Data for four regions of the genome (2382 bp: 12S RNA, $tRNA^{Val}$, 16S RNA, and ND5) were downloaded from GenBank (Appendix C); all sequence data previously were published by Murphy et al. (2002). Sequence data was

available for all rattlesnake species for 12S, save *C. stejnegeri* and *C. lannomi*; data for16S and $tRNA^{Val}$ were not available for *C. transversus*, *C. stejnegeri*, or *C. lannomi*. Sequence data from ND5 were not available for 12 taxa including *C. stejnegeri* (Appendix C). Multiple sequences were available for this data set for four taxa (*C. atrox, C. horridus*, *C. triseriatus*, and *C. willardi*), but only one sequence per taxon was used in the analyses. Sequences were aligned using ClustalX (Thompson et al., 1997), and adjusted by eye using MacClade, version 4.0 (Maddison and Maddison, 2000) with parsimony as the criterion for accepting alternative alignments. Ambiguous alignments (96 bases) were excluded from the analyses. Additional sequence data generated by Murphy et al. (2002) for cytochrome b were not included in the analyses because the possible presence of non-homologous sequences (pseudogenes) was detected during sequence alignment.

Five outgroup taxa were chosen based on previous generic and species-level phylogenetic hypotheses: *Agkistrodon bilineatus*, *A. contortrix*, *A. piscivorus*, *Lachesis muta*, and *Gloydius blomhoffii* (Brattstrom, 1964; Zimmerman and Kilpatrick, 1973; Kraus et al., 1996; Parkinson et al., 1997; Gutberlet and Harvey, 2002; Parkinson et al., 2002). Outgroup data for mensural, meristic, and hemipenial characters were taken from Klauber (1972), Ernst (1982), Solórzano and Cerdas (1986), Campbell and Lamar (1989), Gloyd and Conant (1990), and Werman (1992). Outgroup data for the 177 osteological characters were obtained from 30 osteological specimens; specimens from additional outgroup taxa were examined but not included in the analyses (see Appendix B).

Two additional characters, presence/absence of a rattle and presence/absence of nine enlarged dorsal head scales, were incorporated into the

matrix using data from Klauber (1972), Campbell and Lamar (1989), Gloyd and Conant (1990), and Werman (1992).

Multistate and polymorphic characters

Few characters were not polymorphic in all taxa (each terminal taxon fixed for a particular character state: 14, 15, 30, 53, 153, 200) due to high intraspecific variability in osteological characters.

Five characters could be ordered and were coded using a variation of a majority or modal coding (Wiens, 2000), in which the most common character state for the sampled individuals is assigned for the taxon. In cases where a single character state was not most common for an OTU and instead two character states were seen equally as often (8 out of 175 cases: <5%), both character states were assigned with PAUP's 'interpret multiple states as uncertainty' option invoked. Although this method has not been evaluated for multistate characters, this approach with binary characters can produce results similar to the frequency-bins coding method (Wiens, 1993, 1995; see below), although information about character states found in ≤50% is frequently lost (except for 'tied' states).

One hundred and twenty-nine polymorphic binary characters were coded using the frequency-bins method (Wiens, 1993, 1995). This method partitions the character into 25 ordered bins (*a*-*y*), each representing a range of percentages of the presumed derived state found in a given taxon. Each bin represents a 4% frequency range (save *y*, which represents 5%): state *a* represents the presence of the derived state in 0-3% of specimens examined and state *y* represents presence of the derived state in 96-100% of specimens examined (Table 12).

Thirteen mensural, meristic and qualitative hemipenial characters taken from Klauber (1972) were incorporated by use of a gap-weighting method

(Thiele, 1993), which converts a range of quantitative, overlapping character values into ordered character states, similar to frequency coding. Quantitative values used in this method were the means given by Klauber (1956), with the exception of modal values that were given for numbers of scale rows at midbody. Quantitative characters are not theoretically suitable for use in cladistic analyses (Rae, 1998; Swideriski et al., 1998) and map onto phylogenies similarly to more traditional characters (Thiele, 1993). Many characters described in qualitative language actually represent continuous anatomical variation (Stevens, 1991). The inclusion of these quantitative characters within a cladistic analysis was argued against by Pimentel and Riggins (1987) and Farris (1990), but conversely it has been proposed that many qualitative character states may represent stages of a character continuum that is divided into discrete character states (Thiele, 1993), or "are phenomenologically quantitative" (Stevens, 1991:554). Data were transformed with the function log (x+1) to account for differences in variances between the taxa (unreported in Klauber, 1972), and were then range-standardized using the following equation,

$$x_s = [(x - \min)/(\max\text{-}\min)] \times 24,$$

where min is the lowest and max is the highest mean recorded for that character. Twenty-four represents the number of states between the minimum and maximum values. The standardized means were rounded to the nearest whole integer and assigned a letter code (a = 0, b = 1, c = 2, …y = 24).

Fifty-two polymorphic multistate characters that could not be coded with the frequency bins method were coded using generalized frequency coding or GFC (Smith and Gutberlet, 2001). Both qualitative and quantitative characters can be coded with GFC, taking into account values for each individual of an OTU rather than dealing with structure found in median or mode values (gap-weighting method). A matrix (A) was constructed of taxa by ordered states. Each meristic

count or qualitative character state was treated as its own state and the sample frequency of each ordered state for each taxon was combined to form the matrix. Data from matrix *A* was used to produce matrix *B* of taxa by ordered states, excluding the final character state. The ordered states of matrix *B* are called subcharacters because they represent partitions of a single character/count. Data input for matrix *B* were cumulative frequencies for each subcharacter of each taxon. These cumulative frequencies were the sums of all sample frequencies, within a taxon, to the right of the subcharacter column being filled. The final character state from matrix A was omitted because cumulative frequencies for all taxa would be 0 (no percentage of the sample had a character state/count greater than the final character state/count). Cumulative frequencies for each subcharacter in matrix *B* were replaced by letters corresponding to the frequency bins of Wiens (1995) to form matrix *C* of subcharacters by taxa. The ordered subcharacters of matrix *C* were then input as separate characters in PAUP*, and downweighted so that the cumulative weight of a set of subcharacters (whether informative or non-informative) was equal to a single character. One-hundred and fifty four subcharacters were created from the original fifty-two characters coded via GFC. The computer program CodeThis! (M. Gutberlet et al., 2000), was used to transform raw data into ordered and weighted GFC subcharacters.

Character weights

Because several different coding methods were used in these analyses, it was necessary to apply differential weights to each character to ensure that each character contributed equally to the analysis. All characters were assigned a base weight of 32,767 (the maximum allowed in PAUP*) between extreme character

states because use of the maximum base weight allows for the most exact relative weighting possible (Smith and Gutberlet, 2001). Characters coded with the frequency-bins method, having 24 steps between extreme states, were given a weight of 1365, after dividing the base weight by the maximum number of steps between the extreme states (=32,767/24). The weight of each GFC subcharacter also was divided by the number of steps between extreme states, though this number varied between subcharacters. Additionally, individual subcharacters were downweighted by the number of informative subcharacters used to represent the original character. The five majority-coded characters retained the maximum base weight.

Analyses

Three hundred and eleven morphological characters (including subcharacters created via GFC method) and 2382 molecular characters were entered into PAUP*, version 4.0b10 (Swofford, 2002) and were divided into separate analyses (morphology alone, all molecular alone, ND5 alone, 12S/tRNA^{Val}/16S alone) and one combined analysis (all characters). Data sets were examined via maximum parsimony analyses using heuristic tree searches with 1000 random addition sequences and tree-bisection-reconnection (TBR) branch swapping. Data were evaluated both including and excluding areas of ambiguous alignments. To assess confidence in the most-parsimonious tree(s), a bootstrap analysis (Felsenstein, 1985), with 200 replicate samplings, TBR branch swapping, and five random addition-sequences per bootstrap replicate was performed. Values for consistency index, retention index, and rescaled consistency index are reported (Kluge and Farris, 1969; Farris, 1989).

Non-parametric Templeton tests (Templeton, 1983; Larson, 1994) were performed between the most-parsimonious tree(s) and those hypotheses/phylogenies proposed by Klauber (1956), Brattstrom (1964), Klauber (1972), Foote and MacMahon (1977), Stille (1987), and Murphy et al. (2002) to determine whether or not the data set used to find an optimal tree was significantly incompatible with these alternative trees. Constraint trees for each of the six hypotheses (Figures 16-21) were created using MacClade, version 4.0 (Maddison and Maddison, 2000) and imported into PAUP*. Templeton tests were also conducted between the optimal tree and trees supporting 1) monophyly of *Crotalus* including *S. ravus*, 2) monophyly of *Crotalus* excluding *S. ravus*, and 3) monophyly of both *Crotalus* and *Sistrurus* (including *S. ravus*). These constraints trees also were input using MacClade, and were then imported as constraint trees for a heuristic parsimony analysis, with weights and other assumptions identical to the original analysis of the data save the constraints of rattlesnake generic monophyly. Significance was set to $\alpha = 0.05$. Because of the multiple comparisons using the same data set, sequential Bonferroni (Dunn-Sidák) tests were also performed to reduce potential Type I error (Rice, 1989; Sokal and Rohlf, 1995).

Additional characters

Apomorphies described for the vertebral column of North American pit vipers by various paleontologists (summarized by Holman, 2000) were investigated for inclusion in the present matrix. My initial survey found high levels of intra-individual variation within the vertebral column with none of the published precloacal vertebral apomorphies maintained at either the species- or generic-level. Intra-individual variation within snake vertebral columns was

addressed in only a handful of studies (e.g., Thireau, 1967; LaDuke, 1991a; Head, 2002) and thorough treatment of such variation within rattlesnakes was beyond the scope of the present study.

Developmental timing sequence in the ossification of vertebral elements into the shaker was suggested previously as a potential synapomorphy separating rattlesnake genera (Zimmermann and Pope, 1948). Examination of cleared and stained (C&S) neonate rattlesnake specimens was hampered by lack of accurate age data (days pre- or post-parturition) and general poor quality of C&S material. Again, comprehensive assessment of this single character was beyond the scope of the present study.

RESULTS

Morphology data set alone

A single most-parsimonious tree was found for 35 taxa (Figure 22) of length 35340328 steps (CI = 0.271; RI = 0.436; RC = 0.118). Of the 311 characters from the morphology data set, 292 were parsimony-informative, 3 were constant, and 16 were parsimony uninformative. Bootstrap values indicated support only for *C. intermedius* and *C. transversus* and the monophyly of *Agkistrodon*. None of the Templeton test comparisons demonstrated a significant increase in steps when comparing the best tree estimated from morphology alone to any trees estimated for a given constraint tree after a Bonferroni correction (Table 13).

Molecular data set alone

Sequence data for 477 bp of ND5 were available for 24 taxa in the analyses; no ambiguous sites for alignment were present in the ND5 data. Of the 477 bp, 183 were parsimony-informative, 227 sites were constant, and 67 sites were parsimony-uninformative. Two hundred and forty-nine most-parsimonious trees of length 23133502 steps (CI = 0.472; RI = 0.535; RC = 0.253) were recovered; a majority-rule consensus tree of these 249 trees is shown in Figure 23. Bootstrap values indicated support for several groups including *S. catenatus – S. miliarius* exclusive of *S. ravus* (Figure 23).

A continuous fragment of 1905 bp of sequence data for 12S and 16S rRNA, including the intervening sequence for transfer RNA ($tRNA^{Val}$), was available for 31 taxa in the analyses (Table 13). Of these 1905 bp, 338 were parsimony informative, 1325 sites were constant, and 242 sites were parsimony uninformative. Ninety-six of those sites, however, were ambiguous in their alignments, so analyses were run including and excluding these sites. Of the excluded 96 sites, 48 were parsimony informative, 33 were constant, and 15 were parsimony uninformative. Inclusion of ambiguous sites produced 15 most-parsimonious trees of length 50231811 steps (CI = 0.509; RI = 0.472; RC = 0.240); a majority-rule consensus tree of these 15 trees is present in Figure 24. Bootstrap support maintained many groups including monophyly of *S. catenatus – S. miliarius* exclusive of *S. ravus*. Excluding the 96 ambiguous sites from the analysis produced 12 most-parsimonious trees of length 42269430 steps (CI = 0.526; RI = 0.480; RC = 0.253); a majority-rule consensus tree of these 12 trees is presented as Figure 25. Using the excluded character dataset, bootstrap values for

group and species relationships were similar to values found with the dataset including the ambiguous sites.

Both RNA gene sequences and protein-coding mtDNA gene sequences were combined for two separate analyses, both including and excluding 96 ambiguous sites from the RNA gene sequences. Data were available for 31 taxa (Table 13). Including the 96 ambiguous sites produced a single most-parsimonious tree of length 75560702 steps (CI = 0.485; RI = 0.481; RC = 0.233) (Figure 26). Bootstrap support was high for monophyly of *S. catenatus – S. miliarius* exclusive of *S. ravus*, and for members of the *C. durissus* group (*fide* Murphy et al., 2002) exclusive of *C. enyo*. Excluding the 96 ambiguous sites produced six most-parsimonious trees of length 67401719 steps (CI = 0.493; RI = 0.490; RC = 0.242); a majority-rule consensus tree of these six trees is presented in Figure 27. Bootstrap values for the molecular data set excluding ambiguous sites were almost identical to those found in the complete molecular data set. Subsequent Templeton tests compared the six most-parsimonious trees from the combined molecular data set excluding ambiguous sites to trees constrained to alternative hypotheses proposed in the literature. These most-parsimonious trees showed a significant difference in tree length when compared to trees created using the constraints of six previously reported hypotheses/phylogenies of Klauber (1956, 1972), Brattstrom (1964), Foote and MacMahon (1977), Stille (1987), and Murphy et al. (2002). Trees constraining *Crotalus* monophyly without *S. ravus* or both *Crotalus* and *Sistrurus* monophyly (*S. ravus* with *Sistrurus*) were not significantly different in lengths.

Morphology and molecular data sets combined

All morphological and molecular data were combined for two analyses, with the analyses differing on the inclusion/exclusion of 96 ambiguously-aligned sites from the 12S/tRNA^{Val}/16S sequence. An identical most-parsimonious tree was found for each data set (Figures 28 and 29) with length 114542807 steps with the inclusion of the ambiguous sites (CI = 0.403; RI = 0.434; RC = 0.175) and length 106285523 steps with the exclusion of the ambiguous sites (CI = 0.403; RI = 0.437; RC = 0.176). Bootstrap analyses of each data set produced similar levels of support for several nodes of the tree. Overall bootstrap levels were markedly lower for the combined data set than those shown in the molecular alone data sets. Templeton tests compared the shortest tree using the combined data set excluding ambiguously aligned sites to trees created with the same data set under the constraints of previous hypotheses; all subsequent comparisons were made to this best tree from the combined data set excluding ambiguously aligned sequence sites (Figure 29). All but one of the available comparisons (rattlesnake monophyly and *Crotalus* monophyly with *S. ravus* were found in the shortest tree) were significantly different in tree lengths, including a tree constraining the monophyly of *Crotalus* and *Sistrurus* with *S. ravus* included within *Sistrurus*.

Character support for combined tree (all taxa)

This section briefly details the unambiguous synapomorphies found for several of the major groups, based on the combined analysis using both morphological and molecular characters (excluding the 96 ambiguously aligned characters) (Figure 29). Conditions for reporting these synapomorphies follow Wiens and Reeder (1997): characters are reported to only if they are unambiguously placed at the stem (regardless of optimization criterion, ACCTRAN [Farris, 1970] or DELTRAN [Swofford and Maddison, 1987]); listed

morphological characters must involve a large, unambiguous change in frequency (arbitrarily set at 75%) to emphasize frequency changes with similar weight to changes in DNA sequences (small frequency changes provide evidence of relationships and support for the final tree, although lower frequency changes offer weaker support and are subject to sampling error). If frequency changes met cut-off for both optimization criterion, but were different between those optimizations, the derived ACCTRAN state is listed. Multiple subcharacters for individual characters created by GFC from individual characters may be present in the synapomorphic character list (see Appendix D to convert character numbers to NEXUS numbers). The character list in this section contains an abbreviated description of each character followed in parentheses by the number of the character, a decimal point, and the letter of the derived state. A complete list of character changes for each branch of the combined data tree (Figure 30) is provided in Appendix F.

Using both criteria above, no unambiguous synapomorphies supported the monophyly of *Crotalus* (node 51, including *S. ravus*) or the species group of the *atrox* group (node 64).

The monophyly of the *triseriatus* group (node 39) was supported by no morphological characteristics and 5 DNA synapomorphies; the species of the *viridis* group (node 43) were supported by 22 DNA synapomorphies alone; the species of the *polystictus* group (node 55, *sensu* Murphy et al., 2002) were supported by no morphological characters and 7 DNA synapomorphies.

The sister relationship of *C. tigris* and *C. mitchellii* (node 62, sensu Murphy et al., 2002) was supported by 6 DNA synapomorphies and a single morphological characteristic: vomerine process of the frontal medial to olfactory foramen (221.d). The species of the *durissus* group (node 60) were supported by

17 DNA synapomorphies and a single morphological character: completely fused angular and splenial (100.s, 101.s).

The monophyly of *S. catenatus* and *S. miliarius* (node 45, *S. ravus* found nested elsewhere in the tree) was supported by 30 DNA synapomorphies and six morphological synapomorphies: apex of choanal process of palatine posterior to median tooth socket (31.u), anterolateral maxillary process with blunt, straight vertical face (37.y and 38.y), completely fused angular and splenial (100.y and101.y), tips of posterior and ventral vertical laminae of vomer equidistant caudally (159.u), horizontal shelf projecting anteriorly from ventral margin of olfactory foramen, but less than anterodorsal margin of frontal (208.a), anterodorsal surface of cultiform process extends conspicuously more anterior than anteroventral process, greater than 2x width of anterior vidian canal (308.y).

Nodes supporting membership of all species groups described below, save *C. viridis* and *C. mitchellii* group, were found in trees up to one step (single step between extreme character states equaled 32,767) greater in length using the combined data set, excluding ambiguously-aligned sites (Figure 29).

DISCUSSION

Monophyly of the genera and species groups

The most-parsimonious tree using a combined data set excluding ambiguously aligned sequence sites (Fig. 13) resulted in a mixture of both similarities and departures from previously hypothesized relationships. These

similarities and differences are presented here along with results of the partitioned data sets.

Sistrurus and *C. ravus* – The monophyly of a *Sistrurus* group was supported in the best tree, though not in the traditional sense of three members in the clade (Gloyd, 1940; Klauber, 1956, 1972; Brattstrom, 1964). The sister relationship of *S. miliarius* and *S. catenatus* has strong bootstrap support and typically was supported in all previous morphological (save Stille, 1987) and molecular estimates. Forcing *S. ravus* to remain a member of *Sistrurus* required an additional 375163 steps to the best tree, a significant increase in tree length (Templeton test; P = 0.045). The best tree also supported the placement of *S. catenatus*-*S. miliarius* as the sister group to the rest of the rattlesnakes.

Based on my data, and in agreement with conclusions of Murphy et al. (2002), I support the exclusion of *ravus* from *Sistrurus* and consider this species to be *Crotalus ravus* Cope 1865. Although our respective trees disagree as to the placement of *C. ravus* (basal to *Crotalus* in Murphy estimate vs. nested within *C. triseriatus* group in my best tree), tree length differences were not significantly different between my best tree and the best tree estimated using (outgroup (*miliarius*, *catenatus* (*ravus* (rest of *Crotalus*)))) as a constraint (tree length difference: 182,441; *P* = 0.684).

Several morphological characters have been used to identify the members of *Sistrurus* (Gloyd, 1940; Klauber, 1956, 1972), but these characters (gradual transition of hemipenial spines to calyces and nine large dorsal head scales) are pleisomorphic and can not be used to unite species together. Furthermore, the hemipenial spine-to-calyces condition in *C. ravus* was not known until 1988, when examination revealed an abrupt transition like that seen in *Crotalus* (McCranie, 1988). Tendency of parietal scale subdivision was noted in *S.*

catenatus and *S. miliarius* (Gloyd, 1940; Klauber, 1972) and parietal scale fragmentation with moderate frequency in *C. ravus* (Campbell and Armstrong, 1979).

Previous workers also have identified several vertebral osteology characters that were used to distinguish *Sistrurus* from *Crotalus* (summarized in Holman, 2000; but see Auffenberg, 1963 and Burger, 1971 for additional characters). None of these described vertebral characters could be unambiguously identified within an individual specimen due to high intracolumnar variation (personal observation). Future analyses with careful and concise character definitions (e.g., Head, 2002) may find informative variation between the vertebral columns of these two genera.

Crotalus – The best tree supported the previous estimates of *Crotalus* monophyly, that is neither *S. catenatus* nor *S. miliarius* were placed within the clade. As discussed above, the placement of *C. ravus* within *Crotalus* agrees only with the preferred topology of Murphy et al. (2002). Membership in most species groups of the best tree do not correspond to most of the groups defined by Gloyd (1940), Klauber (1956, 1972), Brattstrom (1964), Foote and MacMahon (1977), and Stille (1987). Comparisons of these hypotheses were presented by Murphy et al. (2002); Table 14 presents species groups as defined by Klauber (1972), Murphy et al. (2002), and this study. Topology of the best tree does not change after removal of all outgroup taxa and using *S. catenatus* and *S. miliarius* to root the tree (sensu Murphy et al., 2002).

Synapomorphies for the genus include an abrupt transition in the hemipenial spines to calyces and the fragmentation of the enlarged dorsal head scales, although the inclusion of *C. ravus* represents a reversal in this latter character. The presence of a distal foramen on the lingual surface of the dentary was purported to be an osteological synapomorphy for *Crotalus* (LaDuke,

1991b), however, all specimens of *C. lepidus* examined for this study lacked this foramen, a reversal of character states.

Crotalus atrox species group – The composition of this species group in my analyses did not differ greatly between the hypotheses of both Klauber (1972) and Murphy et al. (2002), save or the inclusion of *C. stejnegeri* in my analyses. Constraint of membership of the *C. atrox* group as defined by Klauber (1972) and Murphy et al. (2002) when using the combined data set did not significantly increase tree length (both hypotheses with identical increase of 159868 steps; P = 0.0652).

The most-parsimonious trees found only using both 12S/tRNA^{Val}/16S data sets (with and without ambiguously aligned sites) united *C. atrox,* C. *catalinensis, C. ruber,* and *C. tortugensis* with high bootstrap support. *Crotalus adamanteus* was found aligned with a sister group of taxa including *C. scutulatus, C. tigris, C. viridis,* and in some trees *C. mitchellii*. The 249 most-parsimonious trees from the ND5 data set placed *C. adamanteus, C. atrox, C. ruber,* and *C. tortugensis* together (sequence data unavailable for *C. catalinensis* and *C. stejnegeri*) with moderate bootstrap support (68) The high support seen for *C. pusillus* as the sister taxon of *C. ruber* in this same grouping was surprising. The shortest trees from the combined molecular data set placed *C. adamanteus, C. atrox,* C. *catalinensis, C. ruber,* and *C. tortugensis* together, although support for relationships within the species group was marginal. Although support was low for almost every node and set of relationships, the best tree from only the morphology data set placed *C. adamanteus* and *C. atrox* together, but separate from *C. stejnegeri* and *C. tortugensis,* which were together in an adjacent clade; *C. catalinensis* and *C. ruber* were found separately in other parts of the tree.

The placement of *C. stejnegeri* into the *C. atrox* group in these analyses was unexpected because all previous analyses and hypotheses (except Stille, 1987) placed *C. stejnegeri* as a basal member of *Crotalus* based on its unique morphology. *Crotalus stejnegeri*, in addition to having apomorphic hemipenes, has the longest proportional tail of any rattlesnake (long and slender) with one of the smallest, if not the smallest, rattle at the end of the tail. Absence of palatine teeth was a synapomorphy used to previously link *C. stejnegeri* and *C. polystictus* together as basal members of the genus (Klauber, 1956, 1972; Brattstrom, 1964). However, the single skeletal specimen of *C. stejnegeri* that I examined possessed three palatine teeth (UTACV 10499). This species was not represented in the molecular analyses of Murphy et al. (2002) and so was only complete for the morphological characters of this analysis. Additionally, this taxon was represented by a single skeletal specimen in the analysis, a remarkable fact in itself due to the paucity of even fluid preserved *C. stejnegeri* specimens in museum collections (< 20).

No unambiguous morphological or molecular synapomorphies were present for the *C. atrox* clade in the combined data set analysis. Attenuated hemipenes were noted in *C. adamanteus, C. atrox, C. ruber,* and *C. tortugensis*, but this character has not been quantified for the rest of the rattlesnake taxa (Klauber, 1972).

Crotalus catalinensis was considered a sister species of *C. scutulatus* by Klauber (1972), but instead was placed in this analysis within the *C. atrox* group as the basal member, as was suggested by Murphy and Crabtree (1985) and Murphy et al. (2002). The rest of the *C. atrox* group members from this analysis, save *C. stejnegeri*, also were members of this species group in other morphological hypotheses (Gloyd, 1940; Klauber, 1956, 1972; Brattstrom, 1964). In most of these hypotheses, *C. atrox* was the sister taxon of *C. tortugensis*, but in

this study *C. atrox* and *C. adamanteus* are shown to be sister taxa although no unambiguous characters (morphology or molecular) support this node.

Crotalus durissus species group – All five members of this group in my best tree (*C. basiliscus, C. durissus, C. molossus, C. unicolor*, and *C. vegrandis*) were consistently placed into the *C. durissus* group in previous estimates. Differences between previous estimates and my results, however, were due to the exclusion of several species combinations: *C. enyo, C. cerastes*, and *C. horridus* (Klauber, 1956, 1972); *C. horridus* alone (Brattstrom, 1964); *C. enyo* alone (Murphy et al., 2002). Forcing additional taxa into the species group to match group composition defined by Klauber (1956, 1972) significantly increased tree length (491,035 steps; $P = 0.012$) whereas the addition of *C. enyo* or *C. horridus* alone did not significantly increase tree length (*C. enyo*: 179172 steps; $P = 0.076$; *C. horridus*: 168650 steps; $P = 0.354$).

The topology for this species group in the best combined tree was identical to those found in the majority-rule trees for the five molecular partitions. Bootstrap values were generally high, except at for the node at the base of the species group in both 12S/tRNA^{Val}/16S data sets alone (with and without ambiguously aligned sites) (40-45%). Morphology alone provided little evidence to support this group, with meager bootstrap support for any relationships of this species group. The best tree using morphology placed *C. durissus, C. unicolor*, and *C. vegrandis* into a group along with *C. mitchellii, C. stejnegeri*, and *C. tortugensis*; *C. basiliscus* and *C. molossus* were placed into a separate group with *C. polystictus* and *C. scutulatus*.

Presence of a rudimentary left lung historically was used to unite four members of this group. An unpublished manuscript cited by Klauber (1972) lists rudimentary left lungs usually found in *C. basiliscus, C. durissus, C. horridus*,

and C. *molossus*, usually absent in *C. atrox*, *C. cerastes*, *C. enyo*, *C. exsul*, and *C. lepidus*, and invariably absent in 12 other taxa. A vestigial left lung is uncommonly found in *Sistrurus*, is present in all *Agkistrodon*, and uncommonly present or absent in most other pit viper genera (see review by Wallach, 1998). Many forms of variation (intraspecific, ontogenetic, sexual, geographical) are found in certain lung characters, such as presence/absence of the left lung complex with characters being stable in one taxon, but highly variable in other taxa (Wallach, 1998). The presence or absence of this character has not been evaluated systematically in rattlesnakes and may prove informative after scrutiny. However, it will likely be the absence of this character rather than the retention of a primitive state that proves useful in determining species relationships.

Recognition of *C. unicolor* and *C. vegrandis* has been contentious, with a recent paper supporting both species names being synonymized as *C. durissus* (Wüster et al., 2002). Unfortunately, I can not resolve this question because few of the *C. durissus* specimens examined possessed locality information (most were 'no locality' or 'zoo specimen') making direct comparisons to recent estimates impossible.

Scutellation patterns, particularly the arrangement of the two pairs of large head plates anterior to the supraoculars, are characters used to suggest affinities among members of the *C. durissus* group members (Gloyd, 1940; Klauber, 1972). Again, because these scales are thought to be homologous to the large plates of *Sistrurus* and *Agkistrodon*, their shared presence is a symplesiomorphy and does not provide support for group membership.

Crotalus triseriatus species group – Four of the five species found in this species group in my analysis (*C. aquilus*, *C. lepidus*, *C. pusillus*, and *C. triseriatus*) were frequently members of *C. triseriatus* groups in previous estimates, and were the

only species in the *C. triseriatus* species group of Murphy et al. (2002). Additional, different combinations of species were included in other previous estimates, including several other small-sized rattlesnake species, such as *C. intermedius, C. polystictus, C. pricei, C. transversus,* and *C. willardi* (Klauber, 1956, 1972). Constraining the composition of this species group to include these five additional species with *C. aquilus, C. lepidus, C. pusillus,* and *C. triseriatus* (as found in Klauber, 1972) adds a significant increase in tree length to the best tree (1956239 steps; $P = <0.001$).

The position of *C. ravus* within this species group is a novel combination. *Crotalus ravus* was placed as the basal *Crotalus* species by Murphy et al. (2002), with the *C. triseriatus* group the next most basal group. The Murphy et al. (2002) phylogeny places *C. ravus* as the basal member of the clade, rather than basal to the genus. Hemipenial spine number in *C. ravus* (mean = 11.7) is most similar to low spine numbers found in *C. intermedius, C. pusillus,* and *C. triseriatus* (McCranie, 1988). The tendency of *C. ravus* to have nine head plates does not affect the placement of this species in the *C. triseriatus* group, and the fragmentation of the head plates is a synapomorphy of the other four species of the group. The only unambiguous synapomorphies for this clade are five nucleotide sites; there are no morphological synapomorphies for the group.

The morphology-alone data set did not provide any support for the membership of the *C. triseriatus* species group as defined in the combined morphology and molecular analysis. The most-parsimonious tree from the morphology data set did combine six taxa previously considered *C. triseriatus* group members (Gloyd, 1940; Klauber 1956, 1972; Brattstrom, 1964) but there was no bootstrap support for most of the relationships (except that between *C. intermedius, C. transversus,* and *C. pricei*; see *C. viridis* species group below). The ND5 data set found *C. aquilus, C. lepidus,* and *C. triseriatus* to be allied; *C.*

ravus and *C. pusillus* were placed separately and elsewhere in the estimates. The combined molecular analyses as well as the 12S/tRNA^{Val}/16S data followed the topology recovered using the combined morphology and molecular data set, with *C. ravus* consistently placed as the basal member of this species group.

Crotalus viridis species group – The alignment of these five members within the *C. viridis* species group in this analysis was different from all other hypotheses, primarily with the inclusion of *C. pricei*, *C. transversus*, and *C. intermedius*. These three species most often were placed into a *C. triseriatus* species group (Gloyd, 1940; Smith, 1946; Klauber, 1956, 1972) or into a *C. polystictus* species group (Murphy et al., 2002). No skeletal specimens exist for either *C. intermedius* or *C. transversus*, and these taxa were represented in the analysis by fewer than 20 of the morphological characters in addition to the molecular sequence data. Additionally, neither of these two taxa was represented by complete molecular data in the analysis. No morphological synapomorphies united the five members of the *C. viridis* species group although 22 unambiguous DNA apomorphies did support overall group membership.

Of the five species recognized in this species group by the combined morphology and molecular data set, sequence data for ND5 were available only for *C. pricei* and *C. transversus*. These taxa were found to be sister taxa in over 95% of the 249 best trees. Sequence data from 12S/tRNA^{Val}/16S found a similar relationship, though *C. intermedius* was shown to be the sister taxon of *C. transversus*, with *C. pricei* the sister taxon to this group. Both *C. scutulatus* and *C. viridis* are sister taxa elsewhere in the most-parsimonious trees. Combined molecular analyses strongly supports the species group membership found in the combined morphology and molecular analysis. A high bootstrap value from the

morphological analysis also supported the sister species relationship between *C. intermedius* and *C. transversus*, and between these species and *C. pricei*.

Many previous hypotheses placed *C. viridis* and *C. scutulatus* together (Klauber, 1956, 1972; Brattstrom, 1964), although another estimate moved all species, other than *C. viridis* and associated subspecies, out of the species group, making a *C. viridis*-only group (Foote and MacMahon, 1977). Several analyses, primarily molecular, focused solely upon the relationships and taxonomy of the *C. viridis* subspecies, with many of the subspecies most recently being elevated to species (Quinn, 1987; Ashton and de Queiroz, 2000; Pook et al., 2000; Douglas et al., 2002).

Previous morphological estimates placed *C. tigris* and *C. mitchellii* together within the *C. viridis* group (Klauber, 1956, 1972; Brattstrom, 1964), but in this analysis these two taxa were separate from other species groups, and were also recognized as their own species group by Murphy et al. (2002). Adding these two species to this species group significantly increased the tree length of the best tree (1319739 steps; $P = 0.001$). Other estimates included *C. enyo* and *C. cerastes* as sister taxa within this species group (Brattstrom, 1964) and *C. horridus* (Murphy et al., 2002). The forced addition of this latter species to the *C. viridis* species group did not add a significant number of steps (847244 steps; $P = 0.105$).

Crotalus mitchellii species group – The sister-species relationship of *C. tigris* and *C. mitchellii* and the position of this group as the sister clade to the C. *atrox* group was also found in the estimate of Murphy et al. (2002). These two species have often been associated with each other, but they have both generally been placed within the *C. viridis* group (Amaral, 1929; Klauber, 1956, 1972; Brattstrom, 1964). Both taxa were found to have similar head proportions (Klauber, 1972)

and they shared a single derived morphological character (vomerine process of frontal medial to olfactory foramen), along with six DNA synapomorphies.

Despite the single morphological synapomorphy uniting them in the best tree of the combined morphology and molecular data set, *C. mitchellii* or *C. tigris* were not found to be sister taxa in the morphology only data set. *Crotalus tigris* was found to be the sister species of *C. ravus* in the ND5 data set; sequence data for ND5 was unavailable for *C. mitchellii*. Using the 12S/tRNA^{Val}/16S data set, *C. mitchellii* and *C. tigris* were found in clades containing primarily *C. atrox* species group members. Combined molecular analyses showed these two species as sister taxa, and themselves the sister taxon to the *C. atrox* species group.

Crotalus polystictus species group – This species group had only been previously recognized once (Murphy et al., 2002) though species groups from both trees only have two taxa in common. Constraining the monophyly of the group to the six species described by Murphy et al. (2002; Table 14) while using the combined data set required a significant increase in tree length (1283687 steps; $P = 0.001$). This group included sister taxa *C. willardi* and *C. horridus,* a problematic group for Murphy et al. (2002) in that a topology uniting these species together in the *C. viridis* group (Figure 5 in Murphy et al.) "was rejected on the basis of morphological evidence summarized by Klauber (1972) and Knight et al. (1993)." As mentioned above in the *C. durissus* species group section, the presence of a vestigial left lung is not unique to any one previously recognized clade, like *C. durissus*, not is it a synapomorphy for any species group. All members of this species group as defined by Murphy et al. (2002) are small species reaching maximum total lengths less than 1 m; *Crotalus horridus* can grow to in excess of 1.4 m total length

Another member of this *C. polystictus* group, *C. enyo*, had been previously allocated to the *C. durissus* group (Klauber 1956, 1972; Murphy et al., 2002) as well as to the *C. viridis* group (Brattstrom, 1964). *Crotalus polystictus*, with its slender head, has often been thought to be a basal member of the genus (Klauber, 1956, 1972; Brattstrom, 1964), but instead was the sister taxon of *C. enyo* in this analysis.

No support for this species group was found in the ND5 data set. Both *C. enyo* and *C. polystictus* and *C. horridus* and *C. willardi* were consistently present as sets of sister taxa, though these two groups were never allied to each other. Morphology again offered no support for any of these relationships.

Crotalus cerastes – This species was shown as the basal member of *Crotalus* in the best tree, a novel hypothesis for this taxon that has been placed in a diversity of groups within *Crotalus* by previous authors. *Crotalus cerastes* has been allied with *C. enyo* within the *C. viridis* group (Brattstrom, 1964), as well as within the *C. durissus* group as that group's basal member (Klauber, 1956, 1972). *Crotalus cerastes* also has been nested within the *C. triseriatus* group (Foote and MacMahon, 1977), and as a sister species of *C. mitchellii* (Stille, 1987).

Using molecular data sets alone to estimate tree topology (as no ND5 sequence is available for *C. cerastes*) placed the combination of *C. enyo* and C. *polystictus* as the sister taxon of *C. cerastes*, with high bootstrap support. No support was found for this or any other hypothesis for placement of *C. cerastes* in the best tree using the morphology alone data set.

Agkistrodon – Though not an explicit focus of this study, the relationships within *Agkistrodon* can be discussed, primarily on the basis of the morphological data (sequence data was unavailable for *A. bilineatus* for the genomic regions

analyzed in this study). A recent hypothesis placed *A. contortrix* basal to its sister taxa, *A. bilineatus* + *A. piscivorus* (Parkinson et al., 2000). On the contrary, the shortest tree here placed *A. contortrix* and *A. piscivorus* as sister taxa. Overall bootstrap support for this relationship was low, although two unambiguous synapomorphies were found (five or more palatine teeth/teeth sockets and posterior margin of prefrontal without large bulge at posterodorsolateral corner with ~90º angle between posterior edge and bulge). Monophyly of the group was supported with higher bootstrap values and a single unambiguous synapomorphy (extra facet [total of 2] for ectopterygoid articulation on pterygoid).

Previously published molecular-based phylogenies

The cladistic analysis of DNA sequence data (Murphy et al., 2002) was the first species-level phylogeny produced for rattlesnakes based on sequence data. Many of the results of that study are highly concordant with results of this study, not surprising due to the large amount of data shared by both studies. However, questions exist regarding the robustness of the overall Murphy et al. (2002) data set and the criterion used to select a 'preferred' topology from repeated iterations of the analyses. My initial analysis and alignment of the sequence data downloaded from GenBank (see Material and Methods and Murphy et al., 2002 for GenBank accession numbers) revealed problems in the identification and alignment of certain cytochrome b sequences, a protein coding region from mitochondrial DNA. The appearance of single and double base pair (bp) deletions (instead of three bp or entire codon deletions or insertions), along with the presence of regions coding for 'stop' codons in the middle of the 500+ bp fragments may indicate that pseudogenes were sequenced for many rattlesnake taxa rather than the actual genes themselves. Additionally, the decision to

designate a 'preferred' topology over other generated topologies was based on the fact that the preferred tree did not conflict with existing anatomical data. This decision is circular and presupposes that morphological evidence is stronger than molecular evidence, essentially negating much of the need for a molecular phylogeny if morphology is inferred to constrain subsequent topologies.

Intraspecific and osteological variation

Although specific levels or values for intraspecific variation were not reported, workers have discussed the stability of osteological characters in pitvipers:

> "…osteological characters are generally regarded as the most basic or least changeable and hence more likely to indicate relationships than are features of the external morphology…" (Brattstrom, 1964:219)
>
> "[W]e learn [from studies of intraspecific variations in existing rattlesnake species] that osteological characters are relatively stable, followed, in the order of constancy, by anatomical characters (e.g., lungs and hemipenes), head and tail proportionalities, and rattle shape and dimensions. Then come the useful characters of squamation – the most attractive to the taxonomist because they are so easily evaluated, but with evidences of a considerable mutability…Finally, we have the most plastic characters of all – those of color and pattern." (Klauber, 1972:155)

Despite this supposed 'constancy,' over 90% of the osteological characters used in this analysis displayed some level of intraspecific variation. Levels of intraspecific variation for individual characters ranged from only a single individual from a single taxon possessing a character state different than the rest of the individuals from that taxon to multiple individuals from multiple taxa

possessing multiple character states. Examination of skulls taken only from adults limited the influence of ontogenetic variation. Sexual variation in skull characters could not be accounted for because of the lack of data associated with many museum specimens. Intra-individual variation in the vertebral column could not be adequately described, and all vertebral characters were omitted from the analysis. Quantitative levels of intraspecific variation are infrequently addressed and rarely mentioned in most morphological analyses. Reports actually detailing of such variation in squamate systematics and taxonomy have been primarily restricted to saurian families: Anguidae (Campbell and Frost, 1993), Crotaphytidae (McGuire, 1996), Iguanidae (Hollingsworth, 1998), Phrynosomatidae (Wiens, 1995, 1998b; Reeder and Wiens, 1996; Wiens and Reeder, 1997), Polychrotidae (Poe, 1998), and Tropiduridae (Harvey and Gutberlet, 2000). Intraspecific variation also has been reported and used in the phylogenetics of New World pitvipers (Gutberlet, 1998a, 1998b; Gutberlet and Harvey, 2002). More commonly, intraspecific osteological variation is mentioned as part of a larger study focused on a single vertebrate taxon, but even then, only surveys of intraspecific variation were listed have been no discussion of frequency of occurrence (e.g., skulls of lacertid lizards: Barahona and Barbadillo, 1997, 1998; limbs of anurans: Fabrezi, 2001). Detailed analyses are few, but those that quantify and elaborate such intraspecific variation have found patterns that correspond to different (interspecific and intergeneric) phylogenetic levels, along with insights in developmental models (e.g., *Taricha granulosa*: Shubin et al., 1995). The high levels of variation found in rattlesnake cranial osteology (both intra- and interspecific, this study; ontogenetic, personal observation), vertebral osteology (personal observation), scutellation (both intra- and interspecific: Klauber, 1972), dorsal scale microstructure (Stille, 1987) and lung morphology (interspecific, review by Wallach, 1998; intraspecific in *C. viridis*,

Keogh and Wallach, 1999) indicate that morphology may not be particularly informative in determining most of the species-level relationships in this clade. Nevertheless, with few researchers actually reporting levels of intraspecific variation for morphological characters, variation reported here might not be restricted to this group of snakes. A survey of osteological variation in colubrid skulls found the skull of limited use not only in demonstrating major subdivisions within the family Colubridae but also at intergeneric levels (Haines, 1967).

Adequate sample sizes were a problem for this analysis because many taxa were represented by less than five specimens, with some taxa only represented by a single articulated specimen (*C. pusillus*, *C. ravus*, and *C. stejnegeri*). Several other taxa were represented by articulated specimens alone, and three others (*C. catalinensis*, *C. polystictus*, and *C. willardi*) were represented by one disarticulated and several articulated specimens. Nevertheless, the importance and utility of skeletal specimens can not be overstated. Examination of multiple specimens, particularly from underrepresented taxa, was critical in the identification of previously unidentified variations or revisions to published descriptions. An example of these revisions include the posterodorsal process of the dentary of *C. stejnegeri*, previously reported as being shorter than the posteroventral process (Brattstrom, 1964), but the condition was reversed in the single specimen I examined. One of the most important revisions also included the presence of three palatine teeth in *C. stejnegeri*, previously reported as lacking such teeth and interpreted as a synapomorphy uniting *C. polystictus* and *C. stejnegeri*; the absence of palatine teeth is an autapomorphy, unique to *C. polystictus*.

Implications of osteological variation within rattlesnakes

One distinct benefit of the identification of high levels of intraspecific variation is the utility of osteological apomorphies currently used to identify rattlesnakes and other North American pitvipers. Historically, vertebrate paleontologists have used present-day distributions of taxa to refine their search and make their taxon level determination. By using present- day distributions, paleontologists are able to ignore much of the variation, or lack of variation, in bones that exist for a particular taxonomic unit. With a narrower list of possible species, species-level diagnoses are often made via comparisons with one or two recent representatives from each of the possible taxa. Recent workers have highlighted the circularity involved in taxon determinations based on present day distributions and have advocated identification of specimens only to the most diagnosable level (Bell and Gauthier, 2002; Bell et al., in press). This will prove very difficult for the rattlesnakes because no unambiguous synapomorphies, save the fused distal caudal vertebrae (the shaker), were identified for the clade. Unambiguous apomorphies exist for *Agkistrodon* (extra facet [total of 2] for ectopterygoid articulation on pterygoid), and *A. bilineatus* (sphenoid: presence of common foramen for vidian canal and cerebral branch of internal carotid artery). Although no unambiguous osteological synapomorphies were identified within the rattlesnakes, several are indicative but not diagnostic of *Sistrurus* (describe the two and the presence of this state in other taxa). Osteological and allometric variation has largely been ignored as well and should add more levels of complexity to the study of rattlesnake cranial osteology.

Use of polymorphic multistate data and taxa with incomplete data

Literature dealing with taxonomic sampling issues (number of species of a clade needed to recover the correct phylogeny) exists (i.e. Poe, 1998), but missing more often than not are discussions relating to the requisite number of specimens per given taxon needed to address variation within a character. This number (specimens/taxon) would change depending on the type of character and the taxon in which it was being examined. Analogous decisions are applied to molecular analyses; choice of molecular data sets to be used is dependent on the desired level of resolution in the estimated tree. Deeper nodes are addressed with conserved regions, whereas shallower tips are resolved with more variable regions. Establishment of minimum thresholds for character variability has been suggested, such as the incorporation of character states found in 10% or more of a sample (Good, 1988). This presupposes that a minimum sample size can be established for each character, and that adequate numbers of specimens exist for each taxon (Campbell and Frost, 1993). 'Discrete' intraspecifically variable characters have been shown to provide significant phylogenetic information (Wiens, 1995, 1998a); character frequency coding methods (e.g., frequency coding of Wiens, 1993 and generalized frequency coding of Smith and Gutberlet, 2001) divide such variability into discrete characters for analyses. Levels of homoplasy, however, have been found to increase with increased intraspecific variability (Wiens, 1995), as was found in this morphological data set. No osteological characters in this study were identified *a priori* as homoplastic, and their consequent retention likely contributed to the high levels of variability and homoplasy found in the morphological data set.

Many methods and strategies have been developed to deal with polymorphic data in systematic analyses (Wiens, 2000; Smith and Gutberlet, 2001). Rather than use alternative coding methods that have shown lower

accuracies in recovering correctly resolved clades and single shortest trees, such as any-instance, majority, or fixed methods (Wiens, 1998a, 2000), I chose to predominantly use two methods which incorporate frequencies of traits within species, as objections to these methods (e.g., Siddall and Kluge, 1997) has been addressed by Wiens (2000). Additionally, the use of quantitative characters in cladistic analyses has been questioned (Pimentel and Riggins, 1987; Farris, 1990). Several authors have demonstrated that quantitative characters have hierarchical information and are suitable for use in cladistic analyses (Thiele, 1993; Rae, 1998; Swiderski et al., 1998).

Complete data are available for only 23 of the 35 taxa used in the analysis. Wiens and Reeder (1995) indicate that, although including taxa with incomplete data from one or more data partitions decrease the similarity of estimated trees, the decrease appears to be minor. Wiens (1998a) found that the addition of taxa with missing data generally improved phylogenetic accuracy. Conducting analyses after removing those taxa with missing data (taxonomic reduction: Wilkinson, 1995) would defeat the purpose of this study and would provide information for only 23 taxa rather than the 35 taxa presently coded for analyses (counter to the principle of a "total evidence" approach in phylogenetic reconstruction: all available data should be included and explained [Kluge, 1989]). Characters used to estimate relationships between complete taxa also are influenced by character information available for incomplete taxa, so that removal of character information could change hypotheses for relationships of complete taxa. I instead prefer to follow the reasoning of Wiens and Reeder (1995:555): "We prefer to have a phylogenetic hypothesis for these incomplete taxa that is mostly right rather than having no hypothesis for them at all**."**

Evolution/biogeography of rattlesnakes

Most authors point to the highlands of central Mexico as the region that gave rise to the first rattlesnake, with various authors indicating that the slender, long-tailed *Crotalus stejnegeri* probably most closely resembles the early proto-rattlesnake (e.g., Greene, 1997). Molecular divergence estimates (Knight et al., 1993) place the origin of rattlesnakes in the mid-Cenozoic (~30 million years ago), with a split of *Crotalus* and *Sistrurus* some 20 million years ago. Other sources place the first pitvipers in North America by the early Tertiary (Rage, 1982; Gloyd and Conant, 1990), Middle Tertiary (Rage, 1987). Still others place arrival considerably later, well into Late Tertiary (Early Miocene, Holman, 2000; Pliocene ("12 million years ago"; Rubio, 1998). Regardless, the ancestor of this early rattlesnake appears to be linked to one (or several) invasion of Asian crotalines into the New World via the Bering land bridge. Brattstrom (1964) suggests there were two invasions: one line resulting in present day *Bothrops* and *Bothrops*-like pitvipers (*Porthidium*, *Bothriechis*, etc.) and another line producing the rattlesnakes, *Lachesis*, and the New World *Agkistrodon*. Other authors support a single invasion of the New World by Old World crotalines (Kraus et al., 1996; Vidal and Lecointre, 1998; Parkinson, 1999; Vidal et al., 1999; Parkinson et al., 2002).

Klauber (1972) presents the most explicit explanation for the present-day diversification of the rattlesnakes. From a north-central origin in Mexico, he hypothesized that species and species groups moved mainly from south to north, with the exception of the distribution of the northern subspecies of *Crotalus durissus* being attributed to a recent migration from South and Central America. Klauber (1972) hypothesizes that the climatic changes during the Pliocene and Pleistocene enabled many of the now-different species to establish into their present-day ranges. Because more than 25% of all recognized taxa are still found

in the highlands of Mexico, Klauber (1972) further recognized this area as the origin of the rattlesnakes, with the present-day montane and often allopatric distributions a result of climatic shifts and other vicariant events (mountain orogeny) over time.

Gloyd (1940) concurred with Klauber in that the northern highlands of Mexico are likely the center of dispersal of present-day rattlesnake taxa, as the direction of radiation seen in the different species groups all point to an origin in the Mexican highlands. Gloyd also hypothesized that the origin of the rattlesnakes took place "in a period more remote than the Pliocene, or at the latest by the Pleistocene" (1940:249). Brattstrom (1964) took a different view, hypothesizing that the four *Crotalus* species groups differentiated earlier in the Late Eocene or Early Oligocene, with present-day species differentiating and reaching their present ranges by the Middle or Late Pliocene. It is not clear that Brattstrom believed that the rattlesnakes originated from northern Mexico, because his figure of hypothetical rattlesnake distributions over geological time (figure 41: Brattstrom, 1964: 258-259) begins with well established species groups distributed as far north as the Pacific Northwest by the Eocene. Klauber's (1972) phylogeny reflects these zoogeographic events with a basal *Sistrurus* group and a *C. triseriatus* ("montane") group basal to all other *Crotalus*.

The exclusion of *C. ravus* from *Sistrurus* affects some of these biogeographical hypotheses, particularly identification of the Mexican highlands as the origin of the rattlesnakes. Without *C. ravus*, present in the *Sistrurus* species group as defined by Klauber (1972), the basal *Sistrurus* has lost the only member of the group still presently found in the southcentral Mexico; if my combined best tree is correct (Figure 14), several scenarios could explain this discrepancy and still maintain a southern Mexico origin. If *Sistrurus* is the basal and sister taxon to the rest of the rattlesnakes, then rattlesnake genesis could still

have occurred in the Mexican highlands. Unfortunately, the species comprising *Sistrurus* have since altered their geographic distribution or unknown members of the taxon have gone extinct. A paucity of diagnosable crotalid fossils exist to verify either of these hypotheses (Holman, 2000). An alternative hypothesis is that rattlesnakes originated from places other than the southern highlands, and that *S. catenatus* and *S. miliarius* are the basal rattlesnakes.

Crotalus stejnegeri, with its long slender tail and diminutive rattle, could be an intuitive intermediate between *Agkistrodon* (long, slender tail) and the rattlesnakes (shorter, stouter tail). With molecular data is entirely absent for this taxon, my overall analysis of morphology provides no support for this hypothesis. The placement of *C. stejnegeri* in the *C. atrox* group is enigmatic but perhaps understandable due to its placement being based entirely on morphology, and the morphology of a single specimen at that. Sequence data will likely move this taxon elsewhere in subsequent analyses. Continued research in areas such as rattle development and origin (Sisk and Jackson, 1997) and crotalid tail muscle physiology (Moon, 2001), may help to further illuminate this mystery of rattlesnake evolution.

Chapter 5

Interspecific effects of body size on the predatory strike in rattlesnakes (genera *Crotalus* and *Sistrurus*)

INTRODUCTION

Body size plays a major role in the biology and ecology of organisms (Schmidt-Nielsen, 1984; Calder, 1996). Changes in body size have significant implications for an animal's morphology and physiology, with such ontogenetic or evolutionary changes affecting surface-to-volume ratios, metabolic rates, and kinematics (body movements exclusive of their underlying forces). Interspecific comparative studies can identify general constraints imposed by body size by enumerating species differences (e. g., Losos, 1990, Shine, 1994b). Other comparative studies examine species with divergent morphologies or behaviors to look at large-scale changes or constraints within a given system, identifying key innovations or constraints that underlie the evolution of a morphology or behavior (e. g., Reilly and Lauder, 1992; Wainwright and Turingan, 1997).

Broad interspecific analyses can describe suites of behavioral or morphological variation within a given system. Qualitative kinematic patterns of vertebrate feeding have been identified through interspecific studies comparing species, often of similar sizes, but with disparate morphologies and behaviors (e.g., Larsen et al., 1989; Miller and Larsen, 1990; Reilly and Lauder, 1992; Meyers and Nishikawa, 2000). Potential problems can arise in the interpretation

of such interspecific data because of the statistical non-independence of species values used as independent data points (Felsenstein, 1985). Phylogenetic comparative methods (e.g., Martins and Hansen, 1996 and Garland et al., 1999) are frequently used to address potential differences in variation due to historical relatedness in many types of datasets, including developmental timing sequences (e. g., Nunn and Smith 1998; Richardson et al., 2001), metabolic rate (e. g., Nunn and Barton, 2000), muscle physiology (Bonine et al., 2001), and locomotion (e.g., Bonine and Garland, 1999; Tobalske and Dial, 2000; Iriarte-Diaz, 2002; Vanhooydonck et al., 2002).

In making predictions on how size may affect an animal's kinematics, researchers frequently test their results against the theoretical predictions of Hill (1950), whose results on the behavior of whole muscles were extrapolated into a scaling model of whole animal dynamics. Hill's (1950) predictions of kinematic scaling were based on models of isometric (i. e., geometric) change in body size. The power function,

$$Y=aX^{b} \quad (1)$$

can be used to describe relationships between variables that are related to size, where a is the scaling coefficient and b is the scaling exponent (Huxley, 1932; Alexander, 1985). Under a model of isometric growth, a linear measurement (l) of an animal's body is related to its mass (M_b),

$$l=aM_b^{1/3}, \quad (2)$$

or conversely,

$$M_b=al^3 \quad (3)$$

Deviations from this model are termed allometric with exponents either greater (positive allometry) or less (negative allometry) than the value of one expected under isometry. For animal movements, as l and M_b increase under isometry, both timing variables and linear excursions are predicted to increase proportional

to l^1 and $M_b^{0.33}$); velocity (v) is predicted to increase to remain constant or proportional to both l^0 and M_b^0, but acceleration (A) is predicted to decrease proportional to l^{-1} and $M_b^{-1/3}$.

Rattlesnakes (genera *Crotalus* and *Sistrurus*) display substantial body size variation and are an excellent taxon to investigate the effects of body size on feeding kinematics. Only found in the New World, rattlesnakes are a group of more than 30 species for which monophyly is well-supported by a unique morphological attribute (a keratinous rattle at the end of the tail) as well as by molecular analyses (Knight et al., 1993; Kraus et al., 1996, Parkinson, 1999; Murphy et al., 2002). Rattlesnakes are found in a variety of habitats ranging from the xeric North American deserts to the tropical forests of the Amazon Basin; rattlesnakes also are found at a variety of elevations (from below sea level in the Mojave Desert to 3000 m in the mountains around Mexico City). The variation seen in rattlesnake body sizes is remarkable: rattlesnakes display a wide range of adult lengths (e.g., C. *transversus*, 459 mm total length; *C. adamanteus*, 2515 mm total length), with ontogenetic variation spanning two orders of magnitude in several species (Klauber, 1937; Campbell and Lamar, 1989). Rattlesnakes are also venomous and can deliver a proteolytic and hemotoxic venom through their enlarged maxillary fangs, with an entire predatory strike sequence (typically a rapid strike and release) often lasting less than 0.5 sec.

The combination of a rapid and stereotypic predatory strike and the great range of sizes exhibited both ontogenetically and interspecifically presents an opportunity to test, in a phylogenetic context, whether changes in body size have imposed constraints on the evolution of rattlesnake strike performance. Six rattlesnake species (*Crotalus atrox* [data presented previously in Chapter 3], *C. lepidus*, *C. viridis*, *C. willardi*, *Sistrurus catenatus*, and *S. miliarius*) will be used in this study; these six species represent different lineages within the rattlesnake

clade (Murphy et al., 2002), are found in a variety of different habitats, and represent a range of adult body sizes. Four main questions will be investigated using these six rattlesnake species: 1) what are the intraspecific scaling relationships of body size? 2) within adults, what are the interspecific scaling relationships of body size and strike kinematics? 3) can intraspecific scaling patterns of body size and strike kinematics for a single species (*C. atrox*, Chapter 3) be used to predict interspecific scaling patterns? and 4) do strike performance parameters follow predicted models of kinematic scaling, based on either geometric or functional similarity?

Few studies have quantified the effects of body size within a taxon prior to performance comparisons between taxa (e. g., Van Damme et al., 1998; Fish, 1998; Wainwright and Shaw, 1999); this is the first study to address intraspecific differences as well as interspecific differences in kinematic feeding variables for a monophyletic vertebrate taxon within a phylogenetic framework. Ontogenetic scaling relationships of cranial measurements within species often parallel those allometric relationships found among species of fish (Strauss, 1984), lizards (Dodson, 1975), and salamanders (Alberch and Alberch, 1981). Here, an analysis of interspecific acceleration rates will test the hypothesis that interspecific performance variation parallels intraspecific variation. Deviations from the intraspecific allometric trajectory may indicate additional structural or behavioral modifications at the species level.

From body scaling relationships, I will predict the following scaling relationships of predatory strike parameters. If geometric similarity (proportional maintenance of shape with increase in size) were maintained, I would predict kinematic relationships to follow the predictions of Hill (1950). If species were not geometrically similar, I would expect kinematic isometry (both linear displacements and time intervals being scaled equivalents; Alexander, 1985) in

feeding variables (Sweet, 1980; Birch, 1999). Using acceleration as a strike performance parameter, acceleration (*a*) under isometric growth would be proportional to either $M_b^{-1/3}$ or l^{-1} because

$$\text{force } (F) = M_b \times A \quad (4)$$

and F is proportional to l^2 (i.e., cross-sectional muscle area proportional to l^2), and M_b is proportional to l^3, then

$$A = F/M_b \quad (5)$$

which is proportional to either l^{-1} or $M_b^{-1/3}$. If acceleration scales in a corresponding isometric fashion, larger animals would require a relatively longer period of time to complete a strike than would smaller animals as the larger animals' muscle area could not account for the proportionally larger body mass. For larger rattlesnakes to demonstrate kinematic similarity relative to smaller snakes, the cross-sectional muscle area can not scale as predicted by geometric similarity (Sweet, 1980; LaBarbera, 1989). Assuming muscles are equivalent and the same relative mass of the snake moves during the strike, cross-sectional muscle area would need to scale with $M_b^{1.0}$ and not by $M_b^{2/3}$, the latter predicted by geometric similarity.

By answering the questions posed in this study, I will assess whether strike performance is isometrically scaled (larger animals accelerating slower than smaller animals) or allometrically scaled, with similar acceleration values achieved by both small and larger snakes. Additionally, I will be able to determine whether body scaling relationships are accurate predictors of strike scaling relationships in other rattlesnakes. Previous analysis of intraspecific body size and kinematic variation in *Crotalus atrox* (Chapter 3) revealed isometric body scaling patterns which did not predict the allometric kinematic scaling patterns found with video analysis. Scaling analyses in this study, in conjunction

with phylogenetic estimates for the clade, may be important to future studies detailing the role of morphology in aspects of rattlesnake trophic ecology. Scaling changes within species may be indicative of ontogenetic dietary shifts (Mushinsky et al., 1982), and scaling changes between species may indicate historical constraints in feeding ecology which have led to partitioning of resources (for a review see Werner and Gilliam, 1984).

MATERIALS AND METHODS

Morphological analyses

Two hundred and fifty nine preserved rattlesnakes of five species (*C. lepidus, C. viridis, C. willardi, Sistrurus catenatus,* and *S. miliarius*) were examined from four university collections (Table 15; Appendix G). An additional 126 specimens of *Crotalus atrox* examined previously (see Chapter 3) were included in the comparative analyses. Attempts were made to include specimens from a single subspecific taxon or from within a certain region of the overall distribution of the species to reduce potential amount of intraspecific geographic variation (e.g., only specimens from west Texas and New Mexico, subspecies *Crotalus viridis viridis* [= *C. viridis* sensu Douglas et al., 2002], were analyzed for *C. viridis*). Specimens that were not obviously damaged or mutilated were measured and included in analyses; some specimens that were damaged were used only for non-affected variables such as head size and head volume from a posterior trunk-damaged specimen. The overall size range of preserved morphological specimens incorporated the range of live subjects used in

kinematic analyses. Linear measurements of snout-vent and tail length were taken using lengths of string and a wooden meter stick. Linear measurements of the head were taken using digital calipers and included jaw length (distal tip of lower jaw to retroarticular process), head length (mental to transverse line connecting lateral retroarticular processes), width between eyes (at narrowest point), width between retroarticular processes on both mandibles, height of head at snout, height of head at eyes, and the height of head at retroarticular process. Circumferences were measured using a piece of string wrapped around the body at three different points: 25%, 50% and 75% snout-vent length. Cross-sectional area was estimated from the circumferences assuming body shape to be a circle; snake bodies are tubular (Cundall, 1987) or cylindrical (Greene, 1997), although cross-sectional outlines at 1/2 and 3/4 body length may be flattened along ventral surface. Volumes of the head, anterior half of body and whole body were obtained via fluid displacement measured in either a 10 or 50 ml graduated cylinder, with resolutions of 0.1 and 1 ml, respectively. Pre-existing, small ventral incisions in some specimens (if present, typically in the posterior third of body) may have led to underestimates of total volume. Deviations in lengths and weights in the preserved specimens from live values were anticipated, but similar relative deviations were presumed to be present in all specimens (Klauber, 1938).

Mean species values for each morphological variable were calculated for both sexes using the preserved specimens and regressed snout-vent length and body mass. To avoid size-related bias in collection and preservation (Klauber, 1937, 1938), adults of each taxon were used in the calculation of the taxon mean using previous literature estimates for minimum reproductive SVL (Klauber, 1937; Tinkle, 1962; Aldridge, 1979; Fitch and Pisani, 1993; Beaupre, 1995; Farrell et al., 1995; Goldberg and Holycross, 1999; Holycross and Goldberg, 2001; Rosen and Goldberg, 2002).

Video analyses

Kinematic data were obtained from 13 adult snakes from five rattlesnake species (*Crotalus lepidus, C. viridis, C. willardi, Sistrurus catenatus,* and *S. miliarius*) and combined with data from five adult *C. atrox* obtained in a previous study (Table 15; see Chapter 3). The same minimum adult body size estimates used the preserved specimens were used to delineate adults in live snakes. Several of the snake species were collected from localities throughout Texas and New Mexico specifically for this project (*C. atrox, C. viridis* and *S. catenatus*). Other specimens were borrowed from private collections and were either captive-born (*C. willardi*) or long-term captives (*C. lepidus* and *S. miliarius*: 18 months or more). Previous studies show captive-born rattlesnakes to have no differences in locomotor behavior or chemosensory investigation in novel environments relative to wild-caught snakes (Marmie et al., 1990; Chiszar et al., 1993).

Snakes were kept in two isolated but adjacent rooms on the University of Texas at Austin campus, and were maintained in a 12L:12D light cycle at warm (27-30 °C) room temperatures. Each animal was housed individually in one of two differently sized glass terraria measuring either 50 x 30 x 25 cm or 75 x 30 x 30 cm. Snakes were offered food (both live and dead laboratory mice) every two weeks whereas water was given ad libitum. A small cardboard box in each cage served as a daytime refuge. Guidelines and safety features for the care of all rattlesnakes followed Gans and Taub (1964), Murphy and Armstrong (1978), Altimari (1998), as well as guidelines established specifically for this study in conjunction with the University of Texas Animal Care and Welfare Committee (Protocol #99031201). All snakes were in captivity for over four months before feeding trials and filming were initiated, a period of time found not to alter normal

predatory behavior (Kardong, 1993; Alving and Kardong, 1994). Feeding kinematics of the long-term captive snakes were not expected to differ from recently collected animals (Chizar et al., 1993).

The filming arena consisted of an aquarium (90 x 50 x 50 cm), bounded on three-sides by glass and on the fourth by a sheet of pegboard with a small hole cut in the side; the floor was composed of white foam board. A 1-cm grid pattern traced onto film velum was placed onto the back glass pane to enable absolute distance measurements. The snake was placed unrestrained into a partitioned area (50 x 50 x 50 cm) in the test arena 15-30 minutes before filming to allow for acclimatization. Two 15 W fluorescent bulbs were used to backlight the film velum placed on the back of the aquarium, and were left on during the acclimatization period of each snake. A new sheet of 40-lb. brown kraft wrapping paper (Consolidated Plastics Company, Inc.) was secured to the bottom of the cage and was removed after each strike sequence was filmed. A dark 5 mm line was placed on each sheet of kraft paper as a reference for digitizing. Air temperature during filming was kept at 27±0.5°C.

Each strike sequence was recorded at 1000 fps with a Redlake MotionScope 1000S video camera. A Canon ES970 8mm video camcorder was placed above the arena to quantify whether strikes were directed at 60º-120º to the optical axis of the high-speed camera with strikes exceeding this range being excluded. Relative proportion of snake body length kinematically active during the strike also was obtained from this dorsally placed video camcorder. A single 250 W flood lamp was used to illuminate the aquarium 15-20 seconds before introduction of prey items. A single, freshly euthanized mouse was introduced on the end of 62 cm long forceps through the pegboard hole 10-20 seconds following removal of the aquarium partition. The euthanized mouse was moved slowly towards and away from the snake in a plane perpendicular to the camera's optical

axis until the snake struck. All snakes used in this study showed intense interest in the prey item, often characterized by a series of rapid tongue flicks and at times, pursuit of the mouse, resulting in an off-camera strike.

Laboratory mice are known to produce predatory behaviors in snakes equivalent to those elicited by wild rodent prey (genus *Peromyscus*; Kardong, 1993). Dead mice were used in place of live mice in order to remove potentially confounding and unrepeatable responses created by mouse behavior prior to and when struck. Prey item mass varied between 4.5-23.0% of snake mass (mean: 11.0%) to minimize undesired effects on strike behavior such as interpretation of prey item as a threat or holding onto prey item after the strike instead of a quick release (Radcliffe et al., 1980; Kardong, 1986b). Hunger may heighten responsiveness to certain forms of stimuli (Hayes and Duvall, 1991; Hayes, 1993), so all snakes used in this portion of the analyses were fed laboratory mice (both live and dead) on a regular two week basis, which included the regular filming schedule. Snakes were allowed to consume prey struck during filming. Snakes that did not strike during a filming session were not fed until the next filming event, regardless of whether the subsequent filming event was successful.

For each filming attempt, an individual snake was only allowed to strike at a single mouse and was filmed, at a minimum, once every 14 days. The interval between filming attempts was important because of modifications to subsequent rattlesnake strike behaviors due to either previous energy (Lester, 1955) or venom expenditures (O'Connell et al.,1982; Kardong, 1986b; Hayes et al.,1992) . Though venom replacement rates never have been rigorously measured (for a review see Young et al., 2001), estimated rates of venom replenishment range from 3 - 4 days (King, 1941) to two weeks (Oliver, 1944). The interval between filming attempts may also be important because of potential effects of previous strikes on the venom delivery apparatus (e.g. fang breakage: LaDuc, pers. obs.).

The rattlesnake strike was previously divided into four stages: extension, contact, release, and retraction (Kardong and Bels, 1998). The extension stage is defined as the period between initiation of forward movement to target contact, whereas the contact stage is the entire period of prey contact. The release stage begins upon freeing of jaw contact from the target and ends with jaw closure. Retraction involves the period of movement away from the target. Using these definitions, the release and retraction stages overlap greatly with each other, although each deals with a slightly different head/jaw movement. Variables presented in this analysis refer entirely from the extension and contact stages.

Filmed sequences were downloaded to videotape and were analyzed using a MiroMotion frame grabber (Pinnacle Systems GmbH) and the software programs Adobe Premiere 4.2 (Adobe Systems Inc.) and NIH Image 1.62 (developed at the U.S. National Institutes of Health and available on the Internet at http://rsb.info.nih.gov/nih-image/). Analysis of films began at the frame of initiation of forward movement towards the target (including the entire extension stage), and ended at a maximum of five frames after secondary jaw contact. Three distinct points on the snake head were used as landmarks (tip of snout, tip of lower jaw, and mandible-quadrate articulation). Maximum gape angle (MGA) was estimated by measuring the angle between the mandible and a line parallel to the braincase extending through the mandible-quadrate articulation (Cundall and Greene, 2000). Strike distance was determined as the maximum linear distance between snake (tip of snout) and prey in the frame of initial movement towards the target. Four time intervals (time to maximum gape angle, time to contact of mandible with target, and time to contact of upper jaw (palatomaxillary complex) with target, time interval between maximum gape and prey contact) were also recorded. Mean, minimum and maximum times for each of the four timing variables were included in the analyses. Timing values to contact for maximum

and minimum distance (= maximum and minimum distance from strike initiation to prey contact) and timing value to overall maximum gape were also included in the analyses.

Duration of contact with target was initially recorded using the high-speed camera, but was not included in this study because many strike sequences either involved the snake moving both the target and itself off camera, or because contact between snake mandibles and mouse could not be visually confirmed. Contact time could not be reliably estimated from the 8 mm (30 frames/second) camera. Percentage of the snake body kinematically active during the extension stage was estimated from the 8 mm video camera and was defined as the portion of body that moves towards prey item (including recruited body segments). Although this definition may overestimate the portion of the body muscles actually contracting during extension ("active" recruitment of body segments during a strike can only be verified via electromyography), estimates based on this definition were repeatable by multiple observers and were subject to less bias than other estimation definitions.

Velocities and accelerations of the snout were calculated from positional data using QuickSand.008 (Walker, 1997) with a smoothing algorithm (Kosarev-Pantos with odd extension algorithm) recommended by Walker (1998) for use with high-speed film. Maximum velocity and acceleration values were then calculated for each sequence; mean maximum velocity and acceleration values were also calculated for each individual using the mean of maximum values obtained from all strikes from an individual snake. Filming errors are discussed in Chapter 3.

Statistical analyses

Morphological variables within each species were log-transformed and linearly regressed against log SVL, log total volume, and log mass using ordinary least squares (OLS) regression. Log-transformed cranial variables were also regressed against all other cranial variables. Reduced major axis (RMA) slopes were calculated from OLS slopes and correlation coefficients (RMA slope = OLS slope/OLS correlation coefficient; Ricker, 1973; Swartz and Biewener, 1992). Reduced major axis and not OLS regressions were used to test for deviations from isometry, as levels of error in both independent and dependent variables were equivalent (Ricker, 1973; McArdle, 1988, LaBarbara, 1989; Swartz and Biewener, 1992). McArdle (1988) stated that both OLS or RMA regressions could be used if appreciable variation is expected in the independent variable, with RMA results being preferred over OLS if results differ between the regression models. Reduced major axis regressions are considered more robust than OLS when comparing cases of allometric growth (Ricker, 1973). Differences from isometry were determined using the modified test statistic from Clarke (1980: 442). Degrees of freedom (d.f., rounded to nearest whole integer) were calculated using Equation 5.1 from Clarke (1980) with a modification from McArdle (1988: 2332 [$n = N$-2]) and $\alpha = 0.05$. A modified Student's *t*-test was used to test whether regression coefficients for morphological variables differed significantly between the sexes (Zar, 1984: equation 18.1). Because of multiple comparisons using the same data set, sequential Bonferroni (Dunn-Sidák) tests were also performed on all modified *t* statistics to reduce potential Type I errors (Rice, 1989; Sokal and Rohlf, 1995). All statistical tests were done using either StatView 5.0.1 or from formulae manually entered into Microsoft Excel.

To account for statistical non-independence of data using species values due to phylogenetic history, taxon specific data were analyzed using independent contrasts (Felsenstein, 1985; Harvey and Pagel, 1992) in the CAIC program (version 2.6.9; Purvis and Rambaut, 1995). The phylogenetic estimate used as the framework for the calculation of independent contrasts was a parsimony tree based on 2383 base pairs (four mtDNA genes) and 208 morphological characters constructed in Chapter 4, and pruned to the six taxa used in these analyses (Figure 31). Branch lengths were included in the analysis. Taxon data was also analyzed with regression analyses using non-calibrated (assumption of a star phylogeny) values, with differences in slopes between the taxon values and the independent contrast values indicating differences associated with phylogenetic history. Comparisons of slopes calculated from morphological and kinematic data with slopes predicted by geometric similarity would indicate scaling trends for the monophyletic group.

Interspecific morphological data from preserved specimens were analyzed using non-calibrated taxon values and using independent contrasts. All data used in both sets of analyses were log-transformed prior to regression analyses. Regressions using independent contrasts were forced through the origin. Calculated slopes from OLS regressions were tested against predicted isometric slopes using a *t*-test procedure from Zar (1984: equation 17.18). Again, sequential Bonferroni (Dunn-Sidák) tests were performed on all *t*-statistics for multiple and simultaneous comparisons (Rice, 1989; Sokal and Rohlf, 1995).

Because of the intricate nature of the kinematic strike data, data were parsed into three different data sets requiring different assumptions. The first data set, all 75 strikes from 22 individuals, required the assumption that all strikes, even multiple strikes from a single individual, could be treated as independent data points for a statistical analysis. A second data set included the single best

value recorded for multiple strikes from each individual, including multiple individuals per species. The best value for each individual in this data set was either the maximum acceleration or maximum velocity. To address comparisons of strike distance, timing variables, and the extent of body moving during in the strike, two separate values for each variable were used from this second data set, each taken from the strike in which either maximum velocity (= velocity dataset) or maximum acceleration (= acceleration dataset) was recorded for that individual (these two maximum values never characterized the same strike). Values from these three data sets comparing multiple individuals from each species (multiple values per individual, single values per individual [maximum velocity dataset], and single values per individual [maximum acceleration dataset]) were regressed against both SVL and body mass but were not analyzed using independent contrasts.

Species-level analyses were performed on species values calculated each of three different ways. The first of these methods (method 1) used the single maximum velocity and maximum acceleration value recorded for each species. Again, to address comparisons of strike distance, timing variables, and amount of body moving during the strike, two separate values for each variable were used for this first method, one taken from each strike in which either the maximum velocity (= velocity dataset) or maximum acceleration (= acceleration dataset) was recorded. The second method (method 2) utilized a mean value for each variable, including velocity and acceleration, calculated from all strikes within each species. The third method (method 3) utilized the mean value of each individual's best value within a species. Regressions using this third method only involved calculating mean values using maximum velocity and maximum acceleration from each individual. Analyses using the values from the first method were regressed against the SVL and body mass of the individual

producing the best value within each species; analyses using the values from the second and third methods were regressed against both the mean SVL and mean body mass for each species. Species-level analyses were performed with and without calibrating the data by calculating independent contrasts. All values in the kinematic analyses were log-transformed.

Ordinary least squares regression was used in calculating allometric relationships between log-transformed kinematic variables and log-transformed values of SVL and mass. Reduced major axis regression was not used in the kinematic analyses because the majority of the error in the data was in the dependent data (see previous section), considerably greater than one-third the error found in the independent data (~ <1%, data not shown) recommended as a threshold for use of RMA over OLS (McArdle, 1988). Additionally, comparison of RMA regression slopes for kinematic data with those slopes predicted by isometry is not possible for predicted isometric slopes greater than zero. Use of OLS regressions also facilitated comparisons with previous data sets. Calculated slopes from OLS regressions were tested against predicted isometric slopes using a *t*-test procedure from Zar (1984: equation 17.18). Again, sequential Bonferroni (Dunn-Sidák) tests were performed on all *t*-statistics with multiple and simultaneous comparisons (Rice, 1989; Sokal and Rohlf, 1995).

Models of isometry

For morphological analyses, maintenance of geometric similarity was the null model. Although arguments for size-associated change in shape to maintain functional similarity are duly noted (Sweet, 1980), geometric similarity was chosen as the null model because it requires no *a priori* biological assumptions (Emerson and Bramble, 1993). Maintenance of geometric similarity (i.e.,

isometry) was modeled in log-log plots by a slope of one between linear dimensions, a slope of two between a linear dimension and an area dimension, and a slope of three between a linear dimension and a volume (or mass assuming constant density) measurement. Calculated slopes larger than predicted isometric slopes would demonstrate a positive allometry and calculated slope deviations smaller than predicted slopes demonstrate negative allometry. For kinematic analyses, isometric predictions by Hill (1950) served as the null models.

RESULTS

Morphological analyses

Intraspecific comparisons

For gross morphological variables, isometry was the scaling pattern found in almost all regressions (Tables 16-17, 20-21, 24-25, 28-29, 32-33; e.g., Figures 32-35). Several regressions were initially shown to be significantly different from isometry, but the majority of these comparisons were not significant after Bonferroni correction. Negative allometry of head volume was the most common exception to isometry, found versus SVL in male *Crotalus lepidus* and *C. willardi* and in female *C. viridis* and *Sistrurus catenatus* and versus mass in male *C. willardi* and *S. miliarius* and female *C. viridis* and *C. willardi*. Tail length and half body length (minus head volume) increased with positive allometry vs. mass

in male *C. viridis*. Cross-sectional area at 75% body length also increased with positive allometry versus SVL and mass in male *S. catenatus*.

Isometry was also the predominant pattern in cranial variables (Tables 19, 21, 27, 31, 35). No slopes were found to deviate significantly from isometry after Bonferroni correction. In contrast, negative allometry characterized many of the cranial variables (Tables 18, 22, 26, 30, 34). Head length demonstrated negative allometry in both sexes in all species for except *S. miliarius*. Jaw length showed negative allometry in three species of *Crotalus* (in both sexes) but not within *Sistrurus*. Over 75% of regressions between cranial measurements and either SVL or mass in *C. viridis* and *C. willardi* were significantly different from predicted isometric slopes.

Interspecific comparisons

Means were computed for each taxon using only adult specimens (Tables 36-37), with results similar in both sexes. Results were similar in both sexes. Using non-calibrated species values, most of the regression slopes were different than zero when regressed against either body mass or SVL, with many significantly different after Bonferroni correction (Tables 38-39). Regressions of all variables against body size showed negative allometry with respect to predicted isometric slopes (except SVL, which showed positive allometry), but none were significantly different than predicted isometricslopes after Bonferroni correction.

Using independent contrasts, many of the regression slopes were different from zero when contrasts of variables were regressed against either contrasts of body mass or SVL, although only few slopes (many involving volume contrasts) were significantly different from zero after Bonferroni correction (Tables 40-41;

Figures 36-40). Again, almost all slopes showed negative allometry, although none were shown to be significantly different from isometric predictions after Bonferroni correction.

Kinematics

Seventy-five strikes from 22 rattlesnakes were incorporated into the analyses. The numbers of strikes per individual varied from three to six, with 11 individuals having four or more strikes (Tables 42-43). Overall, subjects varied from 86-439 g total mass and 410-855 mm SVL. For the overall dataset (all 75 strikes) maximum velocity and distance were significantly correlated to one other and to all timing variables; maximum acceleration was not correlated with any variable (Table 44).

Velocities and accelerations

None of the slopes resulting from regressions of either maximum velocity or maximum acceleration values against body size, including independent contrasts, were significantly different from zero after Bonferroni correction (Tables 45-48; Figures 42-48). All velocity regression slopes, and 13 of 14 acceleration regression slopes indicated positive allometry with respect to slopes predicted by isometry, but only one of these slopes was found to be significantly different from predicted slopes after Bonferroni correction (maximum acceleration versus SVL; multiple values for multiple individuals). Correlation coefficients for the regressions were less than 0.150 for 13 of 14 regressions of maximum accelerations against body size (Table 45-46). Correlation coefficients were higher within the maximum velocity regressions, except the coefficients for the multiple strikes per individual datasets.

Distance

Many of the regression slopes relating distance against body size were different than zero, with two slopes being significantly different after Bonferroni correction (acceleration dataset; single value per individual, multiple values per species)(Tables 49-50). Regressions of distance against body size showed both positive and negative allometry with respect to the slopes predicted under isometry, but only one slope (accelerations dataset: single value per individual, multiple individuals per species) was significantly different than the predicted isometric slope (positive allometry) after Bonferroni correction.

In the species-level analyses, regressions of mean distance values calculated from all strikes (method 2) showed negative allometry whether using non-calibrated values or independent contrasts. Use of mean distance values calculated from the maximum acceleration of each individual within a species (method 1) resulted in higher slopes than values calculated from the maximum velocity values of each individual within a species, though none of these regressions were significantly different from isometry after the Bonferroni correction.

Percentage of body kinematically active during the strike

None of the18 total regressions of percentage of body moving during the strike against body size were found significantly different than zero (Tables 51-52). The negatively allometric slopes obtained from multiple strikes per individual regressions against body size were significantly different than slope predicted under isometry against both body mass and SVL. One additional slope was significantly different than predicted isometric slopes (acceleration dataset, multiple values per species against SVL).

In the species-level analyses, use of mean distance values calculated from the maximum velocity of each individual within a species (method 1) resulted in higher slopes than values calculated from the maximum acceleration values of each individual within a species. The higher slopes often showed positive allometry with respect to the predicted isometric slopes, though none of these species-level regressions were significantly different from isometry after Bonferroni correction.

Timing variables

Regressions of values for time to maximum gape and time interval between maximum gape and initial prey contact against body size were only significantly different than zero in a single comparison (allometry dataset, multiple values per species)(Tables 53-56). None of the regression slopes were significantly different than slopes predicted under isometry after a Bonferroni correction.

Regressions of values for time to lower jaw contact against body size were significantly different than zero in three comparisons (acceleration dataset, multiple values per species against both body mass and SVL; velocity dataset, multiple values per species against SVL)(Tables 57-58). Three regression slopes were significantly different than predicted isometric slopes after a Bonferroni correction (species-level analysis, mean value [method 2] against SVL, both non-calibrated values and independent contrasts; species-level analysis, mean value [method 2] against body mass, independent contrasts); all three slopes demonstrated negatively allometry with respect to slopes predicted under isometry.

In the species-level analyses, use of the single best timing values calculated from the maximum acceleration of all individuals within a species

(method 1) resulted in higher slopes, which demonstrated positive allometry, than slopes from values calculated from the maximum velocity values of each individual within a species, which primarily showed negative allometry. None of these species-level regressions were significantly different from isometry after the Bonferroni correction.

DISCUSSION

Body scaling

Isometry was found to be as the predominant pattern for all five rattlesnake species in intraspecific regressions for gross morphological variables (Tables 16-17, 20-21, 24-25, 28-29, 32-33). Results for each species closely followed the geometric similarity seen previously in *Crotalus atrox* (Chapter 3). Head volume was the most common exception to isometric growth, showing negative allometry in all five rattlesnakes in this study and in *C. atrox*. These data indicate that head shape does change as rattlesnakes increase in size; juveniles of the six rattlesnake species have proportionally larger heads than adults of the same species. Similar results were presented by Klauber (1938) in an analysis of head dimensions within several rattlesnake species (Table 59, scaling exponents for combined sexes extrapolated from his Table 19). Correlation coefficients for most of the intraspecific regressions were not as high as were found for *C. atrox*, a result likely explained by the reduced sample sizes in the intraspecific datasets in this study. Another potential reason may be due to differential preservation effects in the museum specimens analyzed (Klauber, 1938; Shine, 1991; Chapter

3). For cranial variables, only the correlation coefficients for *C. viridis* and *C. willardi* were comparable to *C. atrox*.

Information on the ontogenetic scaling of body size in snakes is extremely limited, with most studies instead reporting on head sizes in reference either to sexual dimorphism within a species or clade (e.g. Shine, 1991, 1994b), or to taxonomic or geographic variation (e.g. Nakamura and Smith, 1960; King, 1997), or to adaptations for the capturing and ingesting prey (e.g., Greene, 1983; Pough and Groves, 1983). *Vipera berus* (Old World Viperidae) have proportionally longer heads when snakes are shorter (Forsman and Lindell, 1993), and exhibit no sexual dimorphism in head size (Forsman, 1991).

Isometric scaling exponents for overall body morphology were not in agreement with previous findings of positive allometry in *Crotalus atrox* and *C. viridis* (Klauber 1937). Length-weight regressions from Klauber (1937) indicated body mass was proportional to total length$^{3.3}$ for both *C. atrox* and *C. viridis.* The scaling exponents for body mass regressed against SVL for both species in this study, using data combined from the sexes, were significantly different from the scaling exponent of derived by Klauber (*C. atrox*: RMA slope of 3.11, d.f. 84, t = 3.12, P <0.01 using modified test statistic from Clarke, 1980; *C. viridis*: RMA slope of 2.98, d.f. 48, t = 4.74, P <0.001). Two reasons may partially explain the discrepancy between these two sets of values. First, measurements from freshly killed snakes (prior to preservation) were the basis of the data sets collected by Klauber (1937). Subsequent comparisons of measurements of preserved material revealed that total length had decreased by 2% (Klauber, 1938). All specimens used in the present analysis were preserved museum specimens so any bias inherent in using preserved material (distortion, shrinkage) was assumed to be shared equally by all specimens. Second, *C. atrox* examined by Klauber encompassed a larger range of body lengths (0.26-1.68 m) than those specimens

examined for this study (0.24-1.10 m). Perhaps examination of a larger size range of snakes might have changed the allometric coefficients from isometry to positive allometry. Prange and Christman (1976) measured 12 *C. adamanteus* (total length 0.46-1.69 m) and reported an allometric coefficient similar to a value reported by Klauber (1937) for a series of *C. adamanteus* (0.35-1.82 m). Other factors may also be responsible for differences seen between this study and that of Klauber (1937) because the range of total lengths for *C. viridis* examined here (0.27 – 1.08 m) closely followed the range for specimens examined by Klauber (1937)(0.21 – 1.21 m), yet did not produce concordant results. Nevertheless, the preserved specimens examined herein covered the range of body sizes used in the kinematic analyses, and support a model of isometric growth for all variables save those of the head.

Interspecific scaling coefficients for adult morphology, whether estimated via non-calibrated values or via independent contrasts, were similar to many of the intraspecific scaling coefficients, in that the majority of interspecific scaling coefficients were not significantly different from predicted isometric slopes. However, all of the interspecific morphological variables, when regressed against SVL, had lower scaling coefficients than any of the six corresponding intraspecific slopes for a given variable against SVL. A majority of interspecific coefficients regressed against mass also demonstrated a similar bias in being lower than all intraspecific comparisons, but a few coefficients (i.e., snout-vent length vs. mass, both comparisons) were greater than corresponding intraspecific regression coefficients. Although no slopes were significantly different from isometry, the bias in interspecific slope variation (interspecific coefficients predominantly lower than isometry vs. intraspecific coefficients being both higher and lower than isometry) demonstrates a potential difference between these two data sets. Results from these data may be influenced by two factors: low numbers

of independent contrasts or sample sizes and actual differences between inter- and intraspecific regressions. First, the low number of contrasts (independent contrasts = 5) and sample sizes (non-calibrated data = 6) and the corresponding high *t*-test critical values for significance may have contributed to none of the 72 total regression slopes being significantly different from isometry. Comparisons of correlation coefficients and standard error of the mean values between the intra- and interspecific datasets do not reveal any large differences. However, large scale differences in sample size and related ᵗcritical values are present between the two classes of analyses. Second, the tremendous differences in values between certain pairs of intraspecific and interspecific (regardless of phylogenetic treatment) scaling coefficients, such as tail length regressed to either body size metric, are likely valid indicators of differences between intra- and interspecific scaling patterns. The range of values for interspecific slopes of tail length regressed against SVL is 0.158-0.316 (both sexes, both independent contrasts or non-calibrated data); the lowest intraspecific slope of tail length regressed against SVL is 0.718 in female *C. lepidus* (Table 16), but none were significantly different than isometry, like the interspecific scaling coefficients. These data indicate that, although isometric growth is the predominant pattern seen within all rattlesnake species studied, adults of smaller rattlesnake species have proportionally larger tails than adults from larger species. The differences in other interspecific scaling coefficients also imply that adults of smaller species have different relative shapes when compared to adults of larger species. Klauber (1938) observed that smaller rattlesnake species tend to have proportionally larger heads than larger species, concordant with slopes found in this study, though not significantly different from predicted isometric slopes. Klauber (1937) also demonstrated that two smaller species (*C. cerastes* and *C. mitchellii*) had higher scaling coefficients in regressions of body mass to total length than did two larger

species (*C. atrox* and *C. viridis*), which resulted in adults of the former two species being "chunkier, heavier-bodied snakes" than the latter two species.

Kinematic scaling

In comparative studies addressing interspecific relationships between body size and performance, researchers have utilized a variety of performance values as dependent variables in regression analyses. Variations on maximum or best performance values have been used as species values, including mean maximum values using the maximum value recorded for each individual (e g., Bonine and Garland, 1999), mean maximum value recorded over all trials for each species (e. g., Vanhooydonck et al., 2002), and single maximum species value (e.g., Iriarte-Diaz, 2002). Additional studies have employed mean performance values instead of maximum values (Tobalske and Dial, 2000). Use of maximum, rather than mean, performance values is preferred in this type of study where phenotypic variation is reflected in performance capabilities within a species, and over time natural selection would be expected to operate on maximum performance capabilities (Losos et al., 2002). Variables for which maximum performance cannot be assessed, such as variables associated with timing and distance (i.e., difficult to discern the optimal strike distance for any given taxon/individual), mean values are used. Additionally, the use of mean maximum species values recorded over all trials is preferred in this study over alternatives (single maximum species values, mean maximum values using maximum value recorded for each individual) as it prevents any one individual or one trial from biasing a species' representative performance. The use of multiple trials (three to six) for multiple individuals (save *S. miliarius*) to assess maximum performance may also be important for encompassing variation of that variable within a taxon. Scaling

coefficients were similar between non-calibrated values and independent contrasts suggesting that scaling coefficients were little influenced by phylogenetic history.

The overall patterns of isometry found in the intraspecific body scaling comparisons, coupled with the isometry shown in interspecific comparisons, meet the assumptions of geometric similarity required to realistically test the kinematic predictions of Hill (1950). Surprisingly, however, only a single result from the interspecific kinematic analyses was found to resemble intraspecific scaling patterns found in *Crotalus atrox* (Chapter 3): maximum acceleration was size-independent with scaling coefficients not significantly different than zero, though predicted slopes based on rattlesnakes species demonstrating geometric growth were outside the standard error of the mean estimates for the calculated slopes. All other scaling patterns were incongruent because all other interspecific strike variables also demonstrated size independence. Correlation patterns were similar between intra- and interspecific data sets with interspecific correlations showing significant interactions between maximum velocity, strike distance, active body percentages, and timing variables (Table 44). In contrast to the intraspecific data set (Chapter 3, Table 8), maximum acceleration was not significantly correlated with any other strike variable in the interspecific analysis.

Along with the interspecific result of size-independence of maximum velocity is the size-independence of distance (Tables 47-50). Both variables were highly correlated in this analysis, as well as in the intraspecific study, yet their interactions produce substantially different results. In *Crotalus atrox*, maximum velocity showed negative ontogenetic allometry but, with maximum acceleration independent of size, increased velocity was tied to increases in size-dependent strike distance. None of the three timing variables were significantly different from zero. However, two of timing variables were significantly different than predicted isometric slopes (time to maximum gape and time to lower jaw contact;

Tables 55 -57). With all measured kinematic variables being size-independent, the six rattlesnake species in this study demonstrate both functional and kinematic similarity.

As with the body scaling analyses, one potential explanation exists for the kinematic scaling results: none of the scaling coefficients were significantly different than zero due to low numbers of independent contrasts or sample sizes which, along with high *t* critical values, increased the probability of Type II errors (Glantz, 1997). Increased numbers of species or contrasts would conceivably reduce the standard error surrounding some of the regression coefficients and increase the likelihood for significant differences between calculated slopes from slopes of zero or isometry. Rattlesnakes also may truly be kinematically similar, a result which might be further supported by the inclusion of more species or contrasts.

Differential scaling has been suggested for certain groups in which performance and body size does not follow a single linear line, with large taxa following a different scaling trajectory than smaller taxa (Iriarte-Diaz, 2002). There is no immediate support for this trend in this dataset. However neonate metabolic rates in *Crotalus horridus* have been found to be 200 – 400% greater than expectations based on mass-scaling of juvenile or adult rates (Beaupre and Zaidan, 2001). Inclusion of more small-bodied or large-bodied species, or inclusion of large adult *C. atrox* (greater than 1.5 m), could potentially demonstrate this scenario.

Implications for kinematic similarity

Loss of functional similarity would be predicted with maintenance of geometric similarity across species boundaries as shown in both intra- and

interspecific comparisons (Hill, 1950), yet both functional similarity and kinematic similarity are maintained in the predatory strike of rattlesnakes. Maximum acceleration is size-independent both within and across species boundaries (Chapter 3) as well as between predatory and defensive strikes (LaDuc, 2002). Absolute geometric similarity is not maintained in ontogeny, with negative allometry in head size common to both intra- and interspecific comparisons. Negative allometry in head size within a species may confer an advantage to juvenile rattlesnakes with greater fang tip spread (increase in effective striking zone) (Zamudio et al., 2000; Cundall, 2002) due to proportionally larger heads in small snakes which likely increases predatory strike success (Chapter 3). Having larger heads allows young snakes, in which prey size is already constrained by small body size, to consume larger prey than might otherwise be possible (King et al, 1999); smaller rattlesnake species should also benefit from such a situation. The proportional loss of head volume accelerated (and decelerated) during each strike, translated to a decrease in mass (assuming constant density), would also confer a physiological advantage over snakes not demonstrating negative allometry. Interspecific feeding kinematics in snakes have not been previously examined in a phylogenetic context, although interspecific comparisons often allude to potential confounding effects of phylogeny (e.g., Halloy and Burghardt,1990).

Would natural selection favor multiple rattlesnake species to be both geometrically similar and kinematically similar? If the species were allopatrically distributed, perhaps, but some of the species studied are sympatric (*C. atrox* + *C. viridis* + *S. catenatus*, *C. atrox* + *C. viridis*, *C. lepidus* + *C. willardi*). Six sympatric labrid fishes (genus *Halichoeres*) were shown to vary in jaw crushing strength at any given body length (Wainwright, 1988), but in this study the animals are also kinematically similar. Natural selection could operate

on another variable to produce differences between species if feeding kinematics are similar. Different species can occupy different habitats ecologically and temporally, but in a relatively homogeneous habitat, species can occupy different portions of a shared body scaling trajectory, enabling separate species to partition resources, such as food, based on size. Potential problems may arise during ontogeny for species, for example, as juveniles of species A may be the same size as adults of species B for a portion of their lives. *Crotalus atrox* is a widely distributed species found across much of the southwestern U.S. where it can be sympatric and compete for food resources with as many as four other rattlesnake species, in addition to upwards of six to eight other non-venomous snake species. Recent dietary studies have shown that *C. atrox* is a dietary generalist, feeding on mostly on small mammals with smaller proportions of lizard prey throughout ontogeny across its range (C. Spencer, personal communication). Results showing an absence of an ontogenetic shift in feeding kinematics within *C. atrox* complement these dietary data (Chapter 3).

Small changes in head size allometry may allow species to partition resources. Head length is the primary predictor of gape size in snakes (Arnold, 1983): snakes with longer heads can eat larger prey (Forsman and Lindell, 1993). Morphological and dietary data for the gopher snake, *Pituophis catenifer*, showed *P. catenifer* to have a longer head than five sympatric snake species after adjusting for overal size differences (Rodriguez-Robles, 2002). Both *C. willardi* and *C. lepidus* are small montane rattlesnakes often found sympatrically in the mountains of southeastern Arizona and southwestern New Mexico. Dietary specialization by adult *C. lepidus* on lizards appears to be one way these two rattlesnakes can live sympatrically (Holycross et al., 2002a), as *C. willardi* have equal numbers of mice and lizards in their diet (Holycross et al., 2002b).

Differential scaling in snake head size may allow *C. willardi* to eat both types of prey, rather than exclusively lizards.

Crotalus lepidus and *C. willardi* also undergo a large ontogenetic shift in diet with centipedes (genus *Scolependra*) comprising a large portion of both snakes' juvenile diet (Holycross et al., 2002a,b). Anecdotal reports indicate a highly modified strike behavior is used to capture these arthropods (H. McCrystal, personal communication and reported in Holycross et al., 2002b). Interspecific kinematic analyses in this study have only involved the use of mammals as food items. Use of different prey types may require different pre-strike postures and behaviors in rattlesnake species, though documented ontogenetic shifts in diet have lacked corresponding shifts in functional ability in largemouth bass (Richard and Wainwright, 1995).

Are shifts in body size one result of species interactions which lead towards resource partitioning, whereas adaptation is more of an intraspecific response? Additional intraspecific dietary studies are need within rattlesnake species to identify whether concommitant shift take place within species where diet does change, or where other species are in sympatry (but not necessarily conspecific, or even congeners)? These shifts also could occur on a populational level, as shown in the gopher snake, Pituophis catenifer, where many different snake species and prey species occur throughout its geographic distribution (Rodriguez-Robles, 2002).

Kinematic similarity: proximate and ultimate causation

Underlying morphological and physiological shifts not elucidated in the present study may indicate proximate mechanisms for kinematic similarity. Snake epaxial musculature is a highly serialized system, in which each muscle's

insertions and origins across different numbers of vertebral (or rib) elements are interwoven with adjacent sets of muscles. The epaxial musclulature has been hypothesized to be the muscle group primarily responsible for lateral bending of the body (Mosauer, 1935; Gans, 1962). Organization of the epaxial musculature is highly complex with large amounts of interspecific variation present in muscular interconnection arrangements and vertebral insertion lengths for individual muscles (Gasc, 1981; Jayne, 1982). Specific examinations at only two or three points along the trunk have revealed intraspecific as well as intracolumnar differences in the axial musculature (Pregill, 1977; Jayne, 1982).

For rattlesnakes to maintain kinematic similarity despite their apparent geometric similarity (save head volume), muscle groups responsible for providing power during strikes may recruit different amounts or types of muscle through ontogeny. This shift in differential recruitment has been suggested to explain the mass-independence in acceleration in jumping frogs (Emerson, 1978), but such underlying myological changes could not be detected by the gross morphological measurements and comparisons in this study. Delineation, as well as innervation, of functional muscle motor units have only been investigated in a handful of snake taxa, reaching no general consensus being reached (Gray and Lissman, 1950; Jayne, 1988a,b; Gasc et al., 1989; Moon and Gans, 1998; Moon, 2000a,b). Defining functional units of the epaxial musculature is further confounded by the multiple jobs the muscle group may perform in concert to produce a single movement (i.e., elevation of body segments while moving laterally during sidewinding; Jayne, 1988a). Integrated and similarily complex movements also are present in the rattlesnake strike (i.e., elevation of head and neck during rapid forward extension) likely complicating future innervation analyses.

Ultimate causes for kinematic similarity within rattlesnakes may fall into two main categories: phylogenetic relatedness and physiological thresholds in

prey response. As both inter- and intraspecific patterns are found in morphology and likely in feeding kinematics, maintenance of kinematic similarity may have been realized by an ancestor to this clade. Under this scenario, feeding efficiency would have been optimized by the maintenance of kinematic similarity through ontogeny and would be a beneficial trait passed on to descendants. Comparative feeding studies examining patterns of feeding kinematics in less-inclusive snake groups can determine the extent to which similar kinematic patterns have been conserved.

Startle response may be similar throughout rattlesnake prey items, perhaps ultimately governed by a physiological limit or threshold in fast muscle twitch rate. Similarity in twitch response between widely disparate types of vertebrate prey (mammals, birds, fish, lizards), in addition to invertebrates, would be expected for rattlesnakes to maintain functional similarity in their predatory strike. Muscle fiber typing of snakes has been performed for few taxa (Guthe, 1981) with fiber type percentages and distributions potentially varying between taxa and over ontogeny. Perhaps rattlesnakes have exploited aspects of their physiology such that epaxial muscles may act like a spring, storing elastic strain energy to be released in a ballistic motion (Alexander and Bennet-Clark, 1977; Anderson and Pandy, 1993). Rattlesnakes are then able to produce strike accelerations that are impossible to avoid by prey items over short distances. Active stretching of skeletal muscle has been shown to increase passive force enhancement by more than 50% of the total force enhancement (Herzog and Leonard, 2002). Methods such as electromyography (to determine muscle activation sequences) and sonomicrometry (to measure in vivo strain rates), coupled with muscle fiber typing studies, will allow future researchers to interpret and quantify variation found in those epaxial muscles responsible for the incredible acceleration values seen during strikes (Biewener, 2002).

Any advantages gained by rattlesnakes during predatory events, whether due to historical relatedness or physiological thresholds, would be expected for these animals to maintain kinematic similarity over ontogeny. The ability of rattlesnakes to utilize a range of diverse habitats and food resources through their ontogeny and the remarkable variety of habitats populated by various species of rattlesnakes may be further explained through studies that synthesize both the animals' natural and evolutionary history. Future integrated studies of snake size, dietary preferences, biomechanical thresholds, and energetic budgets will clarify mechanisms that allow for sympatry of multiple snake species.

Table 1. Summary statistics and F-ratios from two-way ANOVA results for 13 kinematic variables measured from profiles of two strike types in *Crotalus atrox*. Sample sizes for each individual and definitions of the variables are included in the text. Parenthetical values represent degrees of freedom. * = significance at $P < 0.05$.

	Offensive				Defensive			ANOVA factors		
Variable	N	Mean	S.E.		N	Mean	S.E.	Strike type	Individual	Interaction
Time to lower jaw contact (ms)	12	48.83	5.535		13	50.15	1.548	0.023 (1, 3)	0.283 (3, 17)	0.399 (3, 17)
Time to upper jaw contact (ms)	13	56.77	5.177		13	56.15	2.886	0.020 (1, 3)	0.973 (3, 18)	0.682 (3, 18)
Time to maximum gape: extend stage (ms)	12	43.25	5.510		13	44.77	2.769	0.021 (1, 3)	0.835 (3, 17)	0.601 (3, 17)
Distance from target at for-ward initiation (cm)	13	4.09	1.243		13	9.43	1.548	9.381* (1, 3)	4.217* (3, 18)	2.073 (3, 18)
Amount of body kinematically active (%)	9	28.33	1.193		9	37.55	2.151	13.038*(1, 3)	1.759 (3, 14)	1.328 (3, 14)
Maximum gape angle: extend stage (degrees)	12	85.57	3.992		13	98.37	8.063	2.279 (1, 3)	4.092* (3, 17)	0.982 (3, 17)
Maximum gape angle: retract stage (degrees)	13	146.93	3.025		11	151.31	3.501	2.123 (1, 3)	1.037 (3, 16)	1.755 (3, 16)
Maximum velocity of the snout (m/s)	13	2.61	0.267		13	3.71	0.217	12.980* (1, 3)	3.874* (3, 18)	1.187 (3, 18)
Average velocity: initiation to primary contact (m/s)	13	1.23	0.148		13	2.27	0.179	15.725* (1, 3)	0.247 (3, 18)	0.267 (3, 18)
Average velocity: primary to secondary contact (m/s)	11	2.36	0.272		11	2.77	0.290	0.906 (1, 3)	2.346 (3, 14)	0.136 (3, 14)
Absolute maximum ac-celeration of the snout (m/s^2)	13	326.10	63.561		13	333.77	63.855	0.002 (1, 3)	6.498* (3, 18)	0.260 (3, 18)
Absolute average acceleration: initiation to primary contact (m/s^2)	13	88.94	11.565		13	107.02	9.948	1.617 (1, 3)	4.992* (3, 18)	0.242 (3, 18)
Absolute average acceleration: primary to secondary contact (m/s^2)	11	232.67	45.434		11	235.68	36.961	0.046 (1, 3)	5.137* (3, 14)	0.725 (3, 14)

Table 2. Scaling relationships of nine log-transformed external morphological variables for preserved specimens of *Crotalus atrox* against log-transformed snout–vent length (SVL): tail length, head volume, half–body volume (1/2 volume), half body volume - head volume (1/2–head volume), total volume, estimated cross-sectional area at 25% body length (1/4 cross–sectional area), estimated cross–sectional area at 50% body length (1/2 cross–sectional area), estimated cross–sectional area at 75% body length (3/4 cross–sectional area), total mass. See Methods for complete variable descriptions. $b \pm$ standard error of the mean (s.e.m.), and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against SVL as well as between the sexes from OLS values. Differences from predicted slopes for geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988: $n = N$-2, with $\alpha = 0.05$). * Significant after a Bonferroni correction.

	N	*b* ± s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males								
Tail length	74	0.983 ± 0.030	0.936	1	1.015	50.4	0.224	
Head volume	73	2.166 ± 0.083	0.906	3	2.275	50.2	3.301	$P < 0.005$
1/2 volume	73	2.686 ± 0.110	0.893	3	2.842	50.5	0.604	
1/2 – head volume	72	2.736 ± 0.121	0.879	3	2.917	50.0	0.294	
Total volume	73	2.976 ± 0.077	0.955	3	3.046	49.4	0.263	
1/4 cross-sectional area	74	1.955 ± 0.102	0.835	2	2.139	52.2	0.609	
1/2 cross-sectional area	74	1.936 ± 0.085	0.877	2	1.066	51.4	0.342	
3/4 cross-sectional area	74	1.946 ± 0.083	0.882	2	2.070	51.4	0.370	
Total mass	74	3.068 ± 0.065	0.969	3	3.118	49.8	0.807	
Females								
Tail length	51	0.958 ± 0.051	0.878	1	1.022	35.4	0.193	
Head volume	51	1.821 ± 0.107	0.856	3	1.969	35.7	3.375	$P < 0.005$
1/2 volume	51	2.548 ± 0.100	0.930	3	2.643	34.8	1.455	

Table 2, con't

1/2 – head volume	51	2.687 ± 0.115	0.918	3	2.805	35.0	0.714	
Total volume	51	2.711 ± 0.100	0.937	3	2.801	34.7	0.833	
1/4 cross-sectional area	51	1.616 ± 0.132	0.789	2	1.818	36.6	0.632	
1/2 cross-sectional area	51	1.784 ± 0.117	0.825	2	1.965	36.1	0.129	
3/4 cross-sectional area	51	1.727 ± 0.126	0.794	2	1.938	36.5	0.210	
Total mass	51	3.018 ± 0.106	0.973	3	3.108	34.7	0.451	

Table 3. Scaling relationships of nine log-transformed external morphological variables for preserved specimens of *Crotalus atrox* against log-transformed total mass. Abbreviations are as in Table 2; see Methods for complete character descriptions. b ± standard error of the mean (s.e.m.), and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against total mass as well as between the sexes from OLS values. Differences from predicted slopes for geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988: $n = N$-2, with $\alpha = 0.05$). *Significant with Bonferroni correction.

	N	*b* ± s.e.m.	r^2	Geometric similarity	RMA	d.f.	$t$observed	significance
Males								
Snout-vent length	74	0.316 ± 0.007	0.969	0.333	0.321	49.8	0.570	
Tail length	74	0.313 ± 0.011	0.925	0.333	0.325	50.6	0.190	
Head volume	73	0.699 ± 0.026	0.908	1	0.733	50.2	3.740	$P < 0.001$*
1/2 volume	73	0.877 ± 0.028	0.932	1	0.909	49.8	1.342	
1/2 – head volume	72	0.899 ± 0.032	0.920	1	0.937	49.3	0.830	
Total volume	73	0.965 ± 0.015	0.983	1	0.973	48.9	0.774	
1/4 cross-sectional area	74	0.639 ± 0.029	0.867	0.667	0.686	51.6	0.396	
1/2 cross-sectional area	74	0.638 ± 0.021	0.927	0.667	0.663	50.6	0.052	
3/4 cross-sectional area	74	0.643 ± 0.020	0.937	0.667	0.664	50.4	0.094	
Females								
Snout-vent length	51	0.312 ± 0.011	0.943	0.333	0.321	34.7	0.339	
Tail length	51	0.299 ± 0.020	0.826	0.333	0.329	36.1	0.024	
Head volume	51	0.586 ± 0.034	0.857	1	0.633	35.7	3.678	$P < 0.001$*
1/2 volume	51	0.823 ± 0.030	0.938	1	0.849	34.7	1.994	
1/2 – head volume	51	0.867 ± 0.036	0.923	1	0.902	34.9	1.128	

Table 3, con't

Total volume	51	0.888 ± 0.022	0.972	1	0.901	34.3	1.902	
1/4 cross-sectional area	51	0.537 ± 0.033	0.843	0.667	0.585	35.9	0.926	
1/2 cross-sectional area	51	0.604 ± 0.027	0.913	0.667	0.632	35.0	0.450	
3/4 cross-sectional area	51	0.589 ± 0.029	0.891	0.667	0.624	35.3	0.517	

Table 4. Scaling interrelationships of seven log-transformed external cranial morphological variables for preserved specimens of *Crotalus atrox*. See Methods for complete character descriptions. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against each cranial measurement as well as between the sexes from OLS values. Differences from predicted slopes for geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988: $n = N$-2, with $\alpha = 0.05$). No regressions were significant after Bonferroni correction.

Independent var.	Dependent var.	*N*	$b \pm$ s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males									
Jaw length	Head length	38	0.950 ± 0.028	0.970	1	0.964	26.3	0.544	
Jaw length	Quadrate width	37	1.126 ± 0.073	0.871	1	1.207	26.5	1.345	
Jaw length	Width b/w eyes	36	0.932 ± 0.024	0.979	1	0.942	24.8	1.037	
Jaw length	Snout height	29	0.943 ± 0.070	0.871	1	1.011	20.9	0.067	
Jaw length	Eye height	30	0.848 ± 0.052	0.905	1	0.892	21.3	0.855	
Jaw length	Quadrate height	35	0.933 ± 0.256	0.287	1	1.744	31.5	1.643	
Head length	Quadrate width	37	1.136 ± 0.084	0.839	1	1.240	26.8	1.378	
Head length	Width b/w eyes	36	0.948 ± 0.034	0.957	1	0.969	25.0	0.380	
Head length	Snout height	29	0.971 ± 0.075	0.860	1	1.047	21.0	0.280	
Head length	Eye height	30	0.871 ± 0.055	0.900	1	0.918	21.4	0.623	
Head length	Quadrate height	35	1.110 ± 0.250	0.374	1	1.814	30.3	1.877	
Quadrate width	Width b/w eyes	35	0.731 ± 0.043	0.896	1	0.773	24.9	1.995	
Quadrate width	Snout height	29	0.770 ± 0.068	0.828	1	0.846	21.2	1.441	
Quadrate width	Eye height	30	0.652 ± 0.067	0.773	1	0.742	22.4	1.313	

Table 4, con't

Quadrate width	Quadrate height	34	0.979 ± 0.201	0.426	1	1.499	28.9	0.420	
Width b/w eyes	Snout height	27	0.990 ± 0.087	0.839	1	1.081	19.7	0.414	
Width b/w eyes	Eye height	28	0.902 ± 0.056	0.910	1	0.945	19.9	1.897	
Width b/w eyes	Quadrate height	33	1.115 ± 0.272	0.352	1	1.880	28.9	0.766	
Snout height	Eye height	29	0.810 ± 0.065	0.852	1	0.878	21.0	1.607	
Snout height	Quadrate height	29	1.139 ± 0.242	0.451	1	1.695	24.5	1.818	
Eye height	Quadrate height	30	1.041 ± 0.312	0.284	1	1.953	27.1	1.101	
Females									
Jaw length	Head length	34	0.968 ± 0.023	0.982	1	0.977	23.5	0.430	
Jaw length	Quadrate width	31	1.164 ± 0.077	0.887	1	1.236	22.2	1.472	
Jaw length	Width b/w eyes	33	0.956 ± 0.038	0.953	1	0.980	23.0	0.231	
Jaw length	Snout height	29	0.961 ± 0.061	0.903	1	1.012	20.7	0.083	
Jaw length	Eye height	29	0.927 ± 0.038	0.957	1	0.948	20.3	0.583	
Jaw length	Quadrate height	29	1.040 ± 0.262	0.368	1	1.716	25.3	1.533	
Head length	Quadrate width	31	1.172 ± 0.085	0.867	1	1.259	22.3	1.476	
Head length	Width b/w eyes	33	0.974 ± 0.042	0.946	1	1.001	23.1	0.011	
Head length	Snout height	29	0.981 ± 0.064	0.898	1	1.035	20.7	0.242	
Head length	Eye height	29	0.950 ± 0.039	0.957	1	0.971	20.3	0.316	
Head length	Quadrate height	29	1.162 ± 0.254	0.437	1	1.758	24.6	1.697	
Quadrate width	Width b/w eyes	31	0.749 ± 0.049	0.889	1	0.794	22.2	1.617	
Quadrate width	Snout height	28	0.765 ± 0.058	0.868	1	0.821	20.2	1.204	
Quadrate width	Eye height	28	0.709 ± 0.063	0.830	1	0.778	20.5	1.346	

Table 4, con't

Quadrate width	Quadrate height	28	0.918 ± 0.202	0.442	1	1.380	23.8	0.956	
Width b/w eyes	Snout height	30	0.980 ± 0.070	0.876	1	1.047	21.6	0.300	
Width b/w eyes	Eye height	30	0.950 ± 0.037	0.958	1	0.970	21.0	0.337	
Width b/w eyes	Quadrate height	30	1.139 ± 0.253	0.420	1	1.758	25.6	1.702	
Snout height	Eye height	30	0.874 ± 0.058	0.890	1	0.927	21.5	0.527	
Snout height	Quadrate height	30	1.218 ± 0.218	0.527	1	1.678	24.5	1.729	
Eye height	Quadrate height	30	1.613 ± 0.262	0.413	1	2.512	25.7	2.763	$P < 0.02$

Table 5. Scaling relationships of seven log-transformed external morphological variables for preserved specimens of *Crotalus atrox* against log-transformed snout-vent length (SVL) and log-transformed total mass. See Methods for complete character descriptions. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against SVL and total mass as well as between the sexes from OLS values. Differences from predicted slopes for geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988: $n = N$-2, with $\alpha = 0.05$). No regressions were significant after Bonferroni correction.

	N	*b* ± s.e.m.	r^2	Geometric similarity	RMA	d.f.	$t_{observed}$	significance
Males - SVL								
Jaw length	38	0.844 ± 0.027	0.965	1	0.859	26.3	2.123	$P < 0.05$
Head length	38	0.803 ± 0.034	0.939	1	0.829	26.5	1.983	
Quadrate width	37	0.941 ± 0.072	0.830	1	1.033	26.9	0.202	
Width b/w eyes	36	0.796 ± 0.027	0.962	1	0.811	25.0	2.715	$P < 0.02$
Snout height	29	0.779 ± 0.073	0.808	1	0.867	21.4	0.738	
Eye height	30	0.731 ± 0.038	0.928	1	0.758	21.2	2.370	$P < 0.05$
Quadrate height	35	0.717 ± 0.226	0.234	1	1.484	32.2	1.126	
Males – Total mass								
Jaw length	38	0.273 ± 0.010	0.953	0.333	0.280	26.4	1.987	
Head length	38	0.259 ± 0.013	0.917	0.333	0.271	26.7	1.794	
Quadrate width	37	0.307 ± 0.024	0.820	0.333	0.339	27.0	0.167	
Width b/w eyes	36	0.257 ± 0.010	0.952	0.333	0.263	25.1	2.609	$P < 0.02$
Snout height	29	0.253 ± 0.025	0.797	0.333	0.283	21.5	0.764	
Eye height	30	0.237 ± 0.016	0.890	0.333	0.251	21.5	1.887	
Quadrate height	35	0.238 ± 0.073	0.241	0.333	0.485	32.1	1.101	

Table 5, con't

Females - SVL								
Jaw length	34	0.782 ± 0.055	0.864	1	0.841	24.4	1.115	
Head length	34	0.751 ± 0.059	0.833	1	0.823	24.7	1.174	
Quadrate width	31	0.914 ± 0.085	0.798	1	1.024	22.9	0.121	
Width b/w eyes	34	0.728 ± 0.063	0.806	1	0.811	24.9	1.171	
Snout height	30	0.717 ± 0.084	0.725	1	0.843	22.8	0.751	
Eye height	30	0.676 ± 0.074	0.748	1	0.782	22.6	1.129	
Quadrate height	30	0.833 ± 0.216	0.347	1	1.414	26.4	0.986	
Females – Total mass								
Jaw length	34	0.249 ± 0.015	0.891	0.333	0.264	24.2	0.097	
Head length	34	0.238 ± 0.018	0.851	0.333	0.258	24.6	0.107	
Quadrate width	31	0.289 ± 0.027	0.795	0.333	0.324	22.9	0.008	
Width b/w eyes	34	0.232 ± 0.019	0.828	0.333	0.255	24.8	0.112	
Snout height	30	0.229 ± 0.024	0.763	0.333	0.262	22.4	0.100	
Eye height	30	0.217 ± 0.021	0.793	0.333	0.244	22.4	0.132	
Quadrate height	30	0.249 ± 0.069	0.319	0.333	0.441	26.7	0.126	

Table 6. Raw kinematic data for 20 *Crotalus atrox* used in feeding strike analyses: sex, mass, snout-vent length (SVL), tail length, # strikes, maximal velocity, maximal acceleration, distance of strike. See Methods for complete variable descriptions. Table entries include mean ± 1 standard deviation (range below).

	sex	Mass (g)	SVL (mm)	Tail length (mm)	# of strikes	Maximal velocity (ms^{-1})	Maximal acceleration (ms^{-2})	Strike distance (mm)
KA2	M	99	560	50	1	0.8	159.2	3.5
KA3	F	242	698	43	5	1.8 ± 0.8 (1.0 -3.1)	192.1 ± 67.9 (15.7-298.9)	43.2 ± 32.7 (15.7-100.0)
KA5	M	166	545	79	8	2.1 ± 0.6 (0.7-2.8)	159.5 ± 98.6 (55.6-290.0)	81.1 ± 50.6 (7.4-139.4)
KA8	M	401	835	91	5	2.3 ± 1.1 (0.8-3.2)	147.8 ± 22.8 (135.7-188.4)	85.8 ± 85.2 (13.0-191.2)
KA10	M	125	482	37	5	1.9 ± 0.6 (1.1-2.4)	152.2 ± 12.7 (142.4-173.4)	51.3 ± 48.9 (5.8-114.2)
KA11	M	123	552	52	5	2.0 ± 0.6 (1.5-2.8)	311.9 ± 120.3 (137.5-438.8)	24.6 ± 17.2 (13.7-54.6)
KA12	M	184	595	51	5	2.3 ± 0.9 (1.28-3.14)	218.5 ± 70.0 (130.5-326.6)	68.3 ± 52.8 (9.9-125.6)
KA13	M	439	855	79	5	2.8 ± 1.1 (0.9-3.6)	150.2 ± 37.0 (106.1-185.8)	94.1 ± 50.5 (18.4-152.0)
KA14	M	154	580	40	8	2.0 ± 0.2 (1.7-2.2)	144.4 ± 78.9 (59.3-311.4)	67.1 ± 37.2 (12.8-125.6)
KA15	M	39	360	26	7	0.9 ± 0.2 (0.7-1.3)	167.9 ± 58.8 (127.9-296.2)	16.0 ± 6.2 (3.4-23.0)
KA16	M	46	380	39	7	1.3 ± 0.5 (0.7-2.1)	194.4 ± 121.8 (38.0-408.0)	25.5 ± 19.7 (3.0-64.7)

Table 6, con't

KA19	M	30	340	28	11	1.1 ± 0.2 (0.8-1.5)	105.4 ± 45.6 (63.0-233.7)	35.0 ± 21.7 (6.2-81.5)
KA20	M	176	625	39	6	1.4 ± 0.5 (0.4-1.8)	157.7 ± 56.6 (91.5-230.1)	41.4 ± 24.0 (20.0-79.7)
KA21	M	181	710	55	5	1.6 ± 0.6 (1.0-2.2)	103.1 ± 28.5 (76.7-140.8)	55.0 ± 39.5 (18.0-99.6)
LL3	M	262	812	60	6	2.2 ± 0.4 (1.8-2.8)	173.7 ± 65.8 (99.8-253.2)	60.0 ± 37.0 (24.6-113.7)
LL6	M	73	460	31	1	1.1	117.1	16.7
LL7	F	76	455	39	6	1.8 ± 0.4 (1.3-2.5)	190.3 ± 53.9 (94.2-237.6)	26.5 ± 16.4 (9.2-52.2)
LL9	M	87	510	39	3	1.6 ± 0.3 (1.4-1.9)	189.2 ± 20.3 (166.0-203.9)	27.7 ± 15.0 (10.7-39.1)
LL10	M	43	385	34	2	1.8 ± 1.0 (1.1-2.5)	332.5 ± 147.4 (228.2-436.7)	37.8 ± 28.7 (17.5-58.0)
VV2	F	126	564	36	2	1.5 ± 0.5 (1.1-1.9)	168.3 ± 123.3 (81.1-255.4)	37.3 ± 22.9 (21.1-53.5)

Table 7. Raw kinematic data for 20 *Crotalus atrox* used in feeding strike analyses: maximum gape, time to maximum gape, time interval between maximum gape and initial contact, time to lower jaw contact, time to upper jaw contact, percentage of body kinematically active during strike. See Methods for complete variable descriptions. Table entries include mean ± 1 standard deviation (range below) and sample size (*n*) if different than # of strikes.

	# of strikes	Maximum gape (degrees)	Time to maximum gape (msec)	Interval between gape and contact (msec)	Time to lower contact (msec)	Time to upper contact (msec)	Percent body moving during strike
KA2	1	39.65	20.0	1.0	21.0	40.0	-
KA3	5	64.38 ± 12.34 (49.2-79.43)	44.4 ± 16.1 (25.0-65.0)	4.0 ± 3.2 (1.0-8.0)	49.0 ± 18.3 (26.0-75.0)	60.6 ± 13.2 (46.0-78.0)	34.99 ± 9.33 (21.46-44.90)
KA5	8	53.70 ± 11.65 (35.67-71.49) *n* = 7	55.5 ± 21.5 (22.0-78.0)	8.2 ± 8.7 (1.0-22.0)	70.5 ± 27.1 (26.0-99.0)	72.5 ± 24.3 (34.0-97.0)	41.62 ± 8.35 (30.37-52.01) *n* = 7
KA8	5	45.40 ± 7.40 (37.69-52.44) *n* = 3	65.6 ± 28.9 (21.0-100.0)	3.8 ± 4.8 (1.0-11.0) *n* = 4	72.4 ± 30.4 (27.0-106.0)	79.6 ± 29.4 (37.0-113.0)	40.70 ± 7.91 (30.27-49.47) *n* = 4
KA10	5	55.73 ± 8.71 (49.92-70.53)	47.6 ± 23.4 (20.0-74.0)	5.0 ± 3.1 (1.0-9.0)	51.8 ± 28.1 (21.0-83.0)	55.6 ± 27.0 (21.0-84.0)	47.99 ± 5.18 (43.21-54.04) *n* = 4
KA11	5	57.02 ± 6.42 (51.12-65.79) *n* = 4	34.6 ± 11.9 (19.0-48.0)	2.0 ± 2.2 (1.0-6.0)	39.6 ± 15.2 (23.0-61.0)	48.2 ± 15.2 (33.0-68.0)	48.72 ± 0.44 (48.26-49.32) *n* = 4
KA12	5	48.20 ± 11.08 (36.92-63.02) *n* = 4	43.2 ± 18.9 (19.0-62.0)	4.4 ± 6.0 (1.0-15.0)	53.0 ± 21.5 (20.0-68.0)	53.0 ± 19.8 (24.0-73.0)	33.32 ± 7.37 (27.16-42.68) *n* = 4

Table 7, con't

KA13	5	64.60 ± 4.67 (57.76-67.81) *n* = 4	64.6 ± 29.9 (17.0-99.0)	3.2 ± 3.2 (1.0-9.0)	65.4 ± 27.4 (18.0-86.0)	77.2 ± 28.2 (29.0-103.0)	36.79 ± 6.45 (27.24-41.24) *n* = 4
KA14	8	55.87 ± 8.41 (43.21-68.40)	67.1 ± 24.7 (27.0-102.0)	3.1 ± 2.8 (1.0-9.0)	73.6 ± 33.4 (28.0-137.0)	75.9 ± 27.4 (35.0-120.0)	44.26 ± 7.97 (33.15-53.83) *n* = 7
KA15	7	65.58 ± 10.62 (49.92-78.52)	41.1 ± 9.0 (29.0-56.0)	2.1 ± 2.6 (1.0-8.0)	48.1 ± 10.2 (39.0-66.0)	55.0 ± 10.1 (38.0-70.0)	41.06 ± 6.56 [a]34.27-54.47) *n* = 6
KA16	7	59.30 ± 10.32 (45.00-75.96) *n* = 6	44.0 ± 30.8 (6.0-105.0)	3.5 ± 3.7 (1.0-10.0) *n* = 6	48.8 ± 32.9 (7.0-114.0)	53.8 ± 31.8 (19.0-118.0)	36.09 ± 8.26 (29.29-50.42) *n* = 5
KA19	11	64.38 ± 8.10 (48.89-75.77)	56.6 ± 24.2 (20.0-99.0)	4.2 ± 4.5 (1.0-17.0)	71.4 ± 54.5 (29.0-222.0)	77.6 ± 55.2 (33.0-233.0)	37.83 ± 5.29 (29.83-46.94) *n* = 8
KA20	6	55.27 ± 9.47 (40.91-64.86)	40.5 ± 21.6 (10.0-69.0)	2.5 ± 1.5 (1.0-5.0)	45.8 ± 23.5 (15.0-74.0)	49.7 ± 19.3 (29.0-74.0)	37.84 ± 7.78 (32.24-52.75)
KA21	5	69.87 ± 6.98 (63.19-76.64) *n* = 4	70.0 ± 36.5 (35.0-119.0)	1.8 ± 0.8 (1.0-3.0)	73.0 ± 34.8 (41.0-120.0)	90.4 ± 36.8 (58.0-141.0)	36.0 ± 4.57 (31.96-43.31)
LL3	6	55.63 ± 11.01 (38.07-68.39) *n* = 5	59.7 ± 23.6 (30.0-85.0)	5.7 ± 4.5 (1.0-12.0)	63.3 ± 26.0 (31.0-91.0)	74.8 ± 26.0 (43.0-102.0)	33.82 ± 5.89 (28.82-43.53) *n* = 5
LL6	1	53.08	24.0	1.0	25.0	34.0	-
LL7	6	59.18 ± 7.81 (53.66-64.71) *n* = 2	33.0 ± 11.2 (23.0-49.0) *n* = 4	1.3 ± 0.5 (1.0-2.0)	33.8 ± 11.5 (25.0-56.0)	37.0 ± 10.0 (30.0-56.0)	44.03 ± 3.85 (38.02-47.02) *n* = 5

Table 7, con't

LL9	3	64.26 ± 3.32 (61.92-66.61) *n* = 2	43.0 ± 18.7 (22.0-58.0)	3.5 ± 2.1 (2.0-5.0) *n* = 2	50.3 ± 11.5 (39.0-62.0)	49.7 ± 15.3 (39.0-63.0)	29.53 ± 3.22 (26.16-32.58)
LL10	2	57.68 *n* = 1	41.5 ± 20.5 (27.0-56.0)	1.5 ± 0.7 (1.0-2.0)	47.0 ± 22.6 (31.0-63.0)	50.5 ± 24.7 (33.0-68.0)	48.22 ± 4.67 (44.92-51.52)
VV2	2	68.68 *n* = 1	45.0 ± 17.0 (33.0-57.0)	3.5 ± 3.5 (1.0-6.0)	54.0 ± 28.3 (34.0-74.0)	65.0 ± 32.5 (42.0-88.0)	32.80 *n* = 1

Table 8. Correlated pairs of strike variables taken from product-moment correlations between values from 20 *Crotalus atrox* for seven kinematic variables: maximum velocity, maximum acceleration, strike distance, time to lower jaw contact, time to upper jaw contact, time to maximum gape, % body moving during strike. *Significant after Bonferroni correction.

		F-value	*P*-value
Maximal velocity	Strike distance	88.286	<0.001*
	Time to lower jaw contact	37.852	<0.001*
	Time to upper jaw contact	27.385	<0.001*
	Time to maximum gape	46.938	<0.001*
	Time interval gape-contact	5.659	0.019
Maximal acceleration	Time to lower jaw contact	9.533	0.003*
	Time to upper jaw contact	9.723	0.002*
	Time to maximum gape	10.737	0.001*
Strike distance	Time to lower jaw contact	118.546	<0.001*
	Time to upper jaw contact	102.710	<0.001*
	Time to maximum gape	105.218	<0.001*
	Time interval gape-contact	21.481	<0.001*
Time to lower jaw contact	Time to upper jaw contact	1005.862	<0.001*
	Time to maximum gape	1288.772	<0.001*
	Time interval gape-contact	23.028	<0.001*
Time to upper jaw contact	Time to maximum gape	655.138	<0.001*
	Time interval gape-contact	20.424	<0.001*
Time to maximum gape	Time interval gape-contact	11.183	0.001*

Table 9. Scaling relationships of two kinematic variables from the predatory strikes of 20 *Crotalus atrox* against snout-vent length (SVL) and total mass. All values are log-transformed. Single maximum values attained by each individual over all of its trials were combined and regressed against both SVL and mass. Mean maximum values were calculated for each individual and regressed against both morphological variables. Values for animals that struck <3 times were removed from the data set and regressions were calculated for 16 individuals. $b \pm$ standard error of the mean (s.e.m.), and r^2 calculated from ordinary least squares regression. Differences from geometric similarity were determined using a modified *t*-test from Zar (1984), with degrees of freedom = N-2, and $\alpha = 0.05$. *Significant with Bonferroni correction.

	N	$b \pm$ s.e.m.	r^2	Geometric similarity	^{t}observed	significance
mass						
Maximum acceleration	20	0.115 ± 0.111	0.056	-0.333	1.937	$P < 0.001$*
Mean max. acceleration	20	-0.040 ± 0.092	0.011	-0.333	3.141	$P < 0.01$
Maximum velocity	20	0.310 ± 0.099	0.354	0	3.131	$P < 0.01$
Mean max. velocity	20	0.604 ± 0.075	0.481	0	4.053	$P < 0.001$*
Maximum acceleration	16	-0.120 ± 0.101	0.097	-0.333	2.040	
Mean max. acceleration	16	0.009 ± 0.090	0.001	-0.333	3.767	$P < 0.005$*
Maximum velocity	16	0.303 ± 0.177	0.173	0	1.712	
Mean max. velocity	16	0.316 ± 0.055	0.706	0	5.745	$P < 0.001$*
SVL						
Maximum acceleration	20	-0.383 ± 0.300	0.083	-1	2.057	
Mean max. acceleration	20	-0.142 ± 0.251	0.018	-1	3.418	$P < 0.005$*
Maximum velocity	20	0.719 ± 0.290	0.255	0	2.479	$P < 0.05$
Mean max. velocity	20	0.725 ± 0.225	0.366	0	3.222	$P < 0.005$*
Maximum acceleration	16	-0.375 ± 0.268	0.123	-1	2.332	$P < 0.05$
Mean max. acceleration	16	-0.016 ± 0.243	<0.001	-1	4.049	$P < 0.001$*
Maximum velocity	16	0.891 ± 0.466	0.207	0	1.912	
Mean max. velocity	16	0.782 ± 0.172	0.596	0	4.547	$P < 0.001$*

Table 10. Scaling relationships of three timing variables from the predatory strikes of 20 *Crotalus atrox* against snout-vent length (SVL) and total mass. Abbreviations: time to max gape: time to maximum gape; time to abs. maximum gape: time to absolute maximum gape; time to lower: time to lower jaw contact; time to upper: time to upper jaw contact; interval gape/contact: time interval between maximum gape and initial prey contact; time to abs. min. distance: time to the absolute minimum distance; time to abs. max. distance: time to absolute maximum distance. All values are log-transformed. Mean timing values, timing values for absolute maximum gape, timing values minimum and maximum distances, as well as single minimum and maximum values, were calculated for each individual and regressed against both morphological variables. Values for animals that struck <3 times were removed from the data set and regressions were calculated for 16 individuals. $b \pm$ standard error of the mean (s.e.m.), and r^2 calculated from ordinary least squares regression. Differences from geometric similarity were determined using a modified *t*-test from Zar (1984), with degrees of freedom = N-2, and $\alpha = 0.05$. *Significant with Bonferroni correction.

	N	$b \pm$ s.e.m	r^2	Geometric similarity	^{t}observed	significance
mass						
Mean time to max gape	20	0.182 ± 0.094	0.171	0.333	1.606	
Minimum time to max gape	20	0.060 ± 0.126	0.013	0.333	2.167	$P < 0.05$
Maximum time to max gape	20	0.174 ± 0.140	0.079	0.333	1.136	
Time to abs. maximum gape	20	0.193 ± 0.151	0.083	0.333	0.927	
Mean time to lower	20	0.156 ± 0.101	0.118	0.333	1.752	
Minimum time to lower	20	0.0003 ± 0.124	<0.0001	0.333	2.683	$P < 0.02$
Maximum time to lower	20	0.049 ± 0.163	0.005	0.333	1.742	
Mean time to upper	20	0.156 ± 0.077	0.185	0.333	2.999	$P < 0.05$
Minimum time to upper	20	0.078 ± 0.080	0.051	0.333	3.188	$P < 0.001$*
Maximum time to upper	20	0.048 ± 0.135	0.007	0.333	2.111	$P < 0.05$

Mean interval gape/contact	20	0.271 ± 0.169	0.125	0.333	0.367	
Min. interval gape/contact	20	-0.021 ± 0.049	0.010	0.333	7.224	$P < 0.001$*
Max. interval gape/contact	20	0.304 ± 0.268	0.067	0.333	0.108	
Time to abs. min. distance	20	0.055 ± 0.177	0.005	0.333	1.571	
Time to abs. max. distance	20	0.096 ± 0.138	0.026	0.333	1.717	
Mean time to max gape	16	0.135 ± 0.074	0.194	0.333	2.676	$P < 0.02$
Minimum time to max gape	16	0.110 ± 0.144	0.040	0.333	1.549	
Maximum time to max gape	16	0.080 ± 0.097	0.046	0.333	2.608	$P < 0.02$
Time to abs. maximum gape	16	0.066 ± 0.133	0.017	0.333	2.007	
Mean time to lower	16	0.101 ± 0.078	0.108	0.333	2.974	$P < 0.02$
Minimum time to lower	16	0.026 ± 0.147	0.002	0.333	2.088	
Maximum time to lower	16	-0.077 ± 0.121	0.028	0.333	3.388	$P < 0.005$
Mean time to upper	16	0.119 ± 0.078	0.143	0.333	2.744	$P < 0.02$
Minimum time to upper	16	0.097 ± 0.093	0.073	0.333	2.538	$P < 0.05$
Maximum time to upper	16	-0.051 ± 0.122	0.012	0.333	3.148	$P < 0.01$
Mean interval gape/contact	16	0.138 ± 0.156	0.540	0.333	1.250	
Min. interval gape/contact	16	-0.032 ± 0.059	0.21	0.333	6.186	$P < 0.001$*
Max. interval gape/contact	16	0.044 ± 0.211	0.003	0.333	1.370	
Time to abs. min. distance	16	0.069 ± 0.214	0.007	0.333	1.233	
Time to abs. max. distance	16	-0.002 ± 0.092	0.0001	0.333	3.641	$P < 0.002$
SVL						
Mean time to max gape	20	0.458 ± 0.261	0.146	1	2.077	
Minimum time to max gape	20	0.253 ± 0.341	0.030	1	2.191	$P < 0.05$
Maximum time to max gape	20	0.408 ± 0.387	0.058	1	1.530	
Time to abs. maximum gape	20	0.507 ± 0.415	0.077	1	1.188	
Mean time to lower	20	0.347 ± 0.279	0.090	1	2.244	$P < 0.05$
Minimum time to lower	20	0.111 ± 0.338	0.006	1	2.630	$P < 0.02$

Table 10, con't

Maximum time to lower	20	0.061 ± 0.446	0.001	1	2.105	$P < 0.05$
Mean time to upper	20	0.432 ± 0.211	0.189	1	2.692	$P < 0.02$
Minimum time to upper	20	0.355 ± 0.207	0.141	1	3.116	$P < 0.001$*
Maximum time to upper	20	0.121 ± 0.369	0.006	1	2.382	$P < 0.05$
Mean interval gape/contact	20	0.518 ± 0.478	0.061	1	1.008	
Min. interval gape/contact	20	-0.032 ± 0.133	0.003	1	7.759	$P < 0.001$*
Max. interval gape/contact	20	0.484 ± 0.749	0.023	1	0.689	
Time to abs. min. distance	20	0.195 ± 0.481	0.009	1	1.674	
Time to abs. max. distance	20	0.180 ± 0.379	0.012	1	2.163	$P < 0.05$
Mean time to max gape	16	0.394 ± 0.194	0.227	1	3.124	$P < 0.001$*
Minimum time to max gape	16	0.380 ± 0.382	0.066	1	1.623	
Maximum time to max gape	16	0.256 ± 0.259	0.065	1	2.873	$P < 0.02$
Time to abs. maximum gape	16	0.267 ± 0.355	0.039	1	2.064	
Mean time to lower	16	0.289 ± 0.208	0.121	1	3.418	$P < 0.005$
Minimum time to lower	16	0.193 ± 0.394	0.017	1	2.048	
Maximum time to lower	16	-0.163 ± 0.328	0.017	1	3.546	$P < 0.005$
Mean time to upper	16	0.362 ± 0.204	0.184	1	3.127	$P < 0.01$
Minimum time to upper	16	0.400 ± 0.236	0.170	1	2.542	$P < 0.05$
Maximum time to upper	16	-0.067 ± 0.331	0.003	1	3.224	$P < 0.01$
Mean interval gape/contact	16	0.230 ± 0.426	0.020	1	1.808	
Min. interval gape/contact	16	-0.052 ± 0.159	0.008	1	6.616	$P < 0.001$*
Max. interval gape/contact	16	-0.069 ± 0.570	0.001	1	1.875	
Time to abs. min. distance	16	0.245 ± 0.574	0.013	1	1.315	
Time to abs. max. distance	16	0.013 ± 0.248	0.001	1	3.980	$P < 0.001$*

Table 11. Scaling relationships of three distance and kinematic body length variables from the predatory strikes of 20 *Crotalus atrox* against snout-vent length (SVL) and total mass. Abbreviations: distance: distance of strike; % body kinematic: percentage of body kinematically active during strike. All values are log-transformed. Mean values, as well as single minimum and maximum values, were calculated for each individual and regressed against both morphological variables. Values for animals that struck <3 times were removed from the data set and regressions were calculated for 16 individuals. $b \pm$ standard error of the mean (s.e.m.), and r^2 calculated from ordinary least squares regression. Differences from geometric similarity were determined using a modified *t*-test from Zar (1984), with degrees of freedom = N-2, and $\alpha = 0.05$. *Significant with Bonferroni correction.

	N	$b \pm$ s.e.m	r^2	Geometric similarity	^{t}observed	significance
mass						
Mean distance	20	0.566 ± 0.196	0.315	0.333	1.189	
Minimum distance	20	0.470 ± 0.168	0.302	0.333	0.815	
Maximum distance	20	0.617 ± 0.252	0.250	0.333	1.127	
Mean % body kinematic	18	-0.037 ± 0.046	0.040	0.333	8.043	$P < 0.001$*
Min. % body kinematic	18	-0.091 ± 0.061	0.125	0.333	6.951	$P < 0.001$*
Max. % body kinematic	18	-0.032 ± 0.048	0.027	0.333	7.604	$P < 0.001$*
Mean distance	16	0.535 ± 0.108	0.639	0.333	1.870	
Minimum distance	16	0.606 ± 0.133	0.596	0.333	2.053	
Maximum distance	16	0.522 ± 0.128	0.544	0.333	1.477	
Mean % body kinematic	16	-0.016 ± 0.047	0.009	0.333	7.426	$P < 0.001$*
Min. % body kinematic	16	-0.062 ± 0.065	0.062	0.333	6.077	$P < 0.001$*
Max. % body kinematic	16	-0.025 ± 0.044	0.021	0.333	8.136	$P < 0.001$*
SVL						
Mean distance	20	1.273 ± 0.575	0.214	1	0.475	
Minimum distance	20	1.405 ± 0.440	0.362	1	0.920	

Table 11, con't

Maximum distance	20	1.340 ± 0.729	0.158	1	0.466	
Mean % body kinematic	18	-0.148 ± 0.121	0.086	1	9.488	$P < 0.001$*
Min. % body kinematic	18	-0.271 ± 0.162	0.148	1	7.846	$P < 0.001$*
Max. % body kinematic	18	-0.135 ± 0.128	0.065	1	8.867	$P < 0.001$*
Mean distance	16	1.319 ± 0.329	0.534	1	0.970	
Minimum distance	16	1.805 ± 0.294	0.730	1	2.738	$P < 0.02$
Maximum distance	16	1.264 ± 0.382	0.439	1	0.691	
Mean % body kinematic	16	-0.099 ± 0.124	0.043	1	8.863	$P < 0.001$*
Min. % body kinematic	16	-0.200 ± 0.172	0.088	1	6.977	$P < 0.001$*
Max. % body kinematic	16	-0.116 ± 0.117	0.065	1	9.538	$P < 0.001$*

Table 12. Results of non-parametric Templeton tests comparing hypotheses of rattlesnake relationships to best trees obtained from morphology data alone or morphology plus sequence data (total evidence). * = significance of tied p-value at $P < 0.05$ after Bonferroni correction within each data set (morphology, molecular, morphology and molecular). "–" indicates best tree and best tree under constraint are identical. Multiple values within a cell represent *P* values for multiple most-parsimonious trees created using constraint tree.

Hypothesis	Morphology alone	Molecular alone	Morphology plus molecular
Klauber (1956)	0.025	0.001*	0.001*
Brattstrom (1964)	> 0.05	0.001*	0.001*
Klauber (1972)	0.025	0.001*	0.001*
Foote and MacMahon (1977)	0.025	0.001*	0.001*
Stille (1987)	> 0.05	0.001*	0.001*
Murphy et al. (2002)	> 0.05	0.001*	0.001*
Crotalus monophyly (w/out *ravus*)	> 0.05	> 0.05	> 0.05
Crotalus monophyly (w/ *ravus*)	> 0.05	–	–
Monophyly of both *Crotalus* and *Sistrurus*	> 0.05	0.05, 0.05, 0.025, 0.025	0.001*

Table 13. Frequency bins for use with frequency bins coding and generalized frequency coding (after Wiens, 1995).

Character/subcharacter state	Frequency range (%)
a	0 – 3
b	4 – 7
c	8 – 11
d	12 – 15
e	16 – 19
f	20 – 23
g	24 – 27
h	28 – 31
i	32 – 35
j	36 – 39
k	40 – 43
l	44 – 47
m	48 – 51
n	52 – 55
o	56 – 59
p	60 – 63
q	64 – 67
r	68 – 71
s	72 – 75
t	76 – 79
u	80 – 83
v	84 – 87
w	88 – 91
x	92 – 95
y	96 - 100

Table 14. Rattlesnake species group composition for genus *Crotalus*. Dash indicates taxon not surveyed.

Species group	Klauber 1972	Murphy et al. 2002	this chapter
C. atrox	*adamanteus*	*adamanteus*	*adamanteus*
	atrox	*atrox*	*atrox*
	ruber	*ruber*	*ruber*
	tortugensis	*tortugensis*	*tortugensis*
		catalinensis	*catalinensis*
		–	*stejnegeri*
C. durissus	*basiliscus*	*basiliscus*	*basiliscus*
	cerastes		
	durissus	*durissus*	*durissus*
	enyo	*enyo*	
	horridus		
	molossus	*molossus*	*molossus*
	unicolor	*unicolor*	*unicolor*
	vegrandis	*vegrandis*	*vegrandis*
C. mitchellii		*mitchellii*	*mitchellii*
		tigris	*tigris*
C. polystictus		*cerastes*	
		intermedius	
		polystictus	*polystictus*
		pricei	
		transversus	
		willardi	*willardi*
			enyo
			horridus
C. triseriatus	*intermedius*		
	lepidus	*lepidus*	*lepidus*
	polystictus		
	pricei		
	pusillus	*pusillus*	*pusillus*
	stejnegeri		
	transversus		
	triseriatus	*triseriatus*	*triseriatus*
	willardi		
	lannomi	–	–
	–	*aquilus*	*aquilus*
			ravus
C. viridis	*mitchellii*		
	scutulatus	*scutulatus*	*scutulatus*
	tigris		
	viridis	*viridis*	*viridis*
		horridus	
			intermedius
			pricei
			transversus
C. ravus		*ravus*	
C. cerastes			*cerastes*

Table 15. Sample sizes of taxa used in morphological and kinematic analyses. Both adult and juvenile alcohol preserved specimens were used in morphological analyses; only adult animals, (i.e., greater than minimum reproductive size for respective species) were used in the kinematic analyses.

	# of individuals used	
	Morphology	Kinematics
Crotalus atrox	126	5
Crotalus lepidus	44	2
Crotalus viridis	33	4
Crotalus willardi	70	4
Sistrurus catenatus	45	2
Sistrurus miliarius	67	1

Table 16. Scaling relationships of nine log-transformed external morphological variables for preserved specimens of *Crotalus lepidus* against log-transformed snout-vent length (SVL). Abbreviations are as in Table 2; see methods (Chapter 5) for complete variable descriptions. $b \pm$ standard error of the mean (s.e.m.), and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against SVL as well as between the sexes from OLS values. Differences from predicted slopes for geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988: $n = N$-2, with $\alpha = 0.05$). * Regressions within each sex were significant after Bonferroni correction.

	N	*b* ± s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males								
Tail length	25	1.160 ± 0.120	0.803	1	1.295	18.6	2.850	$P < 0.02$
Head volume	24	1.355 ± 0.216	0.642	3	1.692	18.9	4.592	$P < 0.001$*
1/2 volume	24	3.019 ± 0.260	0.860	3	3.257	17.5	1.053	
1/2 – head volume	23	3.319 ± 0.276	0.873	3	3.554	16.7	2.229	$P < 0.05$
Total volume	23	2.682 ± 0.172	0.920	3	2.797	16.4	1.164	
1/4 cross-sectional area	25	1.363 ± 0.323	0.436	2	2.065	21.3	0.209	
1/2 cross-sectional area	25	1.793 ± 0.222	0.739	2	2.085	19.0	0.399	
3/4 cross-sectional area	25	1.556 ± 0.211	0.703	2	1.857	19.2	0.668	
Total mass	25	2.787 ± 0.240	0.854	3	3.016	18.2	0.069	
Females								
Tail length	19	0.718 ± 0.084	0.812	1	0.797	14.2	2.222	$P < 0.05$
Head volume	19	2.069 ± 0.349	0.675	3	2.520	15.0	1.297	
1/2 volume	19	2.710 ± 0.218	0.901	3	2.856	13.8	0.665	
1/2 – head volume	19	2.838 ± 0.245	0.887	3	3.012	13.9	0.053	
Total volume	19	2.747 ± 0.205	0.913	3	2.873	13.7	0.620	

Table 16, con't

1/4 cross-sectional area	19	1.838 ± 0.383	0.576	2	2.422	15.5	1.246	
1/2 cross-sectional area	19	2.114 ± 0.226	0.837	2	2.310	14.1	1.516	
3/4 cross-sectional area	19	2.217 ± 0.216	0.861	2	2.389	14.0	2.023	
Total mass	19	2.991 ± 0.170	0.948	3	3.071	13.6	0.434	

Table 17. Scaling relationships of nine log-transformed external morphological variables for preserved specimens of *Crotalus lepidus* against log-transformed total mass. Abbreviations are as in Table 2; see methods (Chapter 5) for complete variable descriptions. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against total mass as well as between the sexes from OLS values. Differences from predicted slopes for geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988: $n = N$-2, with $\alpha = 0.05$). * Regressions within each sex were significant after Bonferroni correction.

	N	*b* ± s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males								
Snout-vent length	25	0.307 ± 0.026	0.854	0.333	0.332	18.2	0.087	
Tail length	25	0.362 ± 0.048	0.710	0.333	0.429	19.2	2.396	$P < 0.005$*
Head volume	24	0.425 ± 0.077	0.578	1	0.559	19.4	4.291	$P < 0.05$
1/2 volume	24	1.051 ± 0.062	0.929	1	1.090	17.1	1.555	
1/2 – head volume	23	1.139 ± 0.072	0.922	1	1.186	16.4	2.871	$P < 0.02$
Total volume	23	0.907 ± 0.048	0.945	1	0.933	16.3	1.384	
1/4 cross-sectional area	25	0.514 ± 0.094	0.564	0.667	0.684	20.3	0.270	
1/2 cross-sectional area	25	0.618 ± 0.065	0.799	0.667	0.691	18.6	0.506	
3/4 cross-sectional area	25	0.542 ± 0.061	0.775	0.667	0.616	18.7	0.714	
Females								
Snout-vent length	19	0.317 ± 0.018	0.948	0.333	0.325	13.6	0.258	
Tail length	19	0.235 ± 0.027	0.822	0.333	0.259	14.2	2.432	$P < 0.05$
Head volume	19	0.679 ± 0.112	0.685	1	0.821	14.9	1.491	
1/2 volume	19	0.892 ± 0.064	0.92	1	0.930	13.7	1.086	

Table 17, con't

1/2 – head volume	19	0.933 ± 0.073	0.906	1	1.001	13.8	0.015	
Total volume	19	0.917 ± 0.045	0.961	1	0.936	13.5	1.427	
1/4 cross-sectional area	19	0.633 ± 0.114	0.644	0.667	0.789	15.1	1.272	
1/2 cross-sectional area	19	0.700 ± 0.067	0.866	0.667	0.752	14.0	1.511	
3/4 cross-sectional area	19	0.723 ± 0.070	0.864	0.667	0.777	14.0	1.884	

Table 18. Scaling relationships of seven log-transformed external morphological variables for preserved specimens of *Crotalus lepidus* against log-transformed snout-vent length (SVL) and log-transformed total mass. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against SVL and total mass as well as between the sexes from OLS values. Differences from predicted slopes under geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988; $n = N$-2, with $\alpha = 0.05$). * Regressions for each independent variable within each sex were significant after Bonferroni correction.

	N	$b \pm$ s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males - SVL								
Jaw length	17	0.638 ± 0.058	0.890	1	0.676	12.5	4.725	$P < 0.001$*
Head length	17	0.640 ± 0.048	0.923	1	0.666	12.3	5.860	$P < 0.001$*
Quadrate width	17	0.737 ± 0.103	0.774	1	0.838	13.0	1.492	
Width between eyes	17	0.771 ± 0.116	0.748	1	0.891	13.1	0.917	
Snout height	17	0.517 ± 0.136	0.490	1	0.739	14.5	1.697	
Eye height	17	0.543 ± 0.107	0.631	1	0.684	13.7	2.502	$P < 0.05$
Quadrate height	17	0.504 ± 0.140	0.464	1	0.740	14.6	1.644	
Males – Total mass								
Jaw length	17	0.119 ± 0.024	0.817	0.333	0.220	12.8	3.786	$P < 0.005$*
Head length	17	0.200 ± 0.022	0.850	0.333	0.217	12.6	4.333	$P < 0.001$*
Quadrate width	17	0.235 ± 0.036	0.744	0.333	0.272	13.1	1.510	
Width between eyes	17	0.247 ± 0.039	0.724	0.333	0.290	13.2	0.977	
Snout height	17	0.144 ± 0.050	0.361	0.333	0.240	15.2	1.602	
Eye height	17	0.176 ± 0.035	0.629	0.333	0.221	13.7	2.605	$P < 0.05$

Table 18, con't

Quadrate height	17	0.164 ± 0.046	0.463	0.333	0.241	14.6	1.712	
Females - SVL								
Jaw length	16	0.628 ± 0.034	0.960	1	0.641	11.5	8.618	$P < 0.001$*
Head length	16	0.657 ± 0.035	0.962	1	0.700	11.5	7.965	$P < 0.001$*
Quadrate width	16	0.699 ± 0.062	0.901	1	0.737	11.7	3.764	$P < 0.005$*
Width between eyes	16	0.600 ± 0.044	0.929	1	0.622	11.6	6.892	$P < 0.001$*
Snout height	16	0.470 ± 0.096	0.630	1	0.592	12.9	3.339	$P < 0.005$*
Eye height	16	0.666 ± 0.082	0.826	1	0.733	12.0	2.888	$P < 0.02$*
Quadrate height	16	0.763 ± 0.102	0.801	1	0.852	12.1	1.385	
Females – Total mass								
Jaw length	16	0.198 ± 0.020	0.873	0.333	0.212	11.8	4.810	$P < 0.001$*
Head length	16	0.211 ± 0.018	0.911	0.333	0.221	11.7	5.195	$P < 0.001$*
Quadrate width	16	0.220 ± 0.028	0.817	0.333	0.243	12.1	2.757	$P < 0.02$
Width between eyes	16	0.190 ± 0.021	0.850	0.333	0.206	11.9	4.709	$P < 0.001$*
Snout height	16	0.150 ± 0.034	0.588	0.333	0.196	13.1	3.157	$P < 0.01$
Eye height	16	0.217 ± 0.028	0.806	0.333	0.242	12.1	2.740	$P < 0.02$
Quadrate height	16	0.256 ± 0.032	0.824	0.333	0.282	12.0	1.453	

Table 19. Scaling interrelationships of seven log-transformed external cranial morphological variables for preserved specimens of *Crotalus lepidus*. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against each cranial measurement as well as between the sexes from OLS values. Differences from predicted slopes under geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988: $n = N$-2, with $\alpha = 0.05$). No regressions were significant after a Bonferroni correction.

Independent var.	Dependent var.	*N*	$b \pm$ s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males									
Jaw length	Head length	17	0.967 ± 0.049	0.963	1	1.046	12.1	1.249	
Jaw length	Quadrate width	17	1.085 ± 0.155	0.766	1	1.148	11.9	1.401	
Jaw length	Width b/w eyes	17	1.203 ± 0.141	0.830	1	0.972	11.8	0.326	
Jaw length	Snout height	17	0.705 ± 0.216	0.415	1	0.924	12.9	0.501	
Jaw length	Eye height	17	0.856 ± 0.140	0.714	1	1.143	12.0	1.300	
Jaw length	Quadrate height	17	0.778 ± 0.199	0.505	1	1.331	12.0	2.669	$P < 0.025$
Head length	Quadrate width	17	1.078 ± 0.167	0.734	1	1.258	13.2	1.779	
Head length	Width b/w eyes	17	1.192 ± 0.157	0.793	1	1.339	12.9	2.569	$P < 0.05$
Head length	Snout height	17	0.726 ± 0.217	0.428	1	1.110	14.8	0.552	
Head length	Eye height	17	0.870 ± 0.141	0.718	1	1.026	13.2	0.193	
Head length	Quadrate height	17	0.824 ± 0.192	0.551	1	1.110	14.1	0.626	
Quadrate width	Width b/w eyes	17	1.017 ± 0.081	0.913	1	1.065	12.4	0.853	
Quadrate width	Snout height	17	0.671 ± 0.148	0.579	1	0.882	14.0	0.776	
Quadrate width	Eye height	17	0.604 ± 0.142	0.547	1	0.817	14.1	1.199	

Table 19, con't

Quadrate width	Quadrate height	17	0.518 ± 0.184	0.345	1	0.882	15.4	0.618	
Width b/w eyes	Snout height	17	0.661 ± 0.129	0.637	1	0.828	13.7	1.250	
Width b/w eyes	Eye height	17	0.644 ± 0.108	0.705	1	0.768	13.3	1.948	
Width b/w eyes	Quadrate height	17	0.588 ± 0.151	0.503	1	0.829	14.4	1.062	
Snout height	Eye height	17	0.714 ± 0.152	0.565	1	0.926	14.0	0.466	
Snout height	Quadrate height	17	0.745 ± 0.172	0.554	1	1.001	14.1	0.008	
Eye height	Quadrate height	17	1.024 ± 0.089	0.898	1	1.080	12.4	0.966	
Females									
Jaw length	Head length	16	1.035 ± 0.038	0.981	1	1.045	11.4	1.249	
Jaw length	Quadrate width	16	1.061 ± 0.117	0.854	1	1.148	11.9	1.401	
Jaw length	Width b/w eyes	16	0.917 ± 0.086	0.890	1	0.972	11.8	0.326	
Jaw length	Snout height	16	0.734 ± 0.150	0.631	1	0.924	12.9	0.501	
Jaw length	Eye height	16	1.049 ± 0.121	0.842	1	1.143	12.0	1.300	
Jaw length	Quadrate height	16	1.211 ± 0.147	0.828	1	1.331	12.0	2.669	$P < 0.025$
Head length	Quadrate width	16	1.006 ± 0.118	0.838	1	1.098	12.0	0.902	
Head length	Width b/w eyes	16	0.874 ± 0.085	0.883	1	0.930	11.8	0.824	
Head length	Snout height	16	0.715 ± 0.139	0.654	1	0.884	12.8	0.813	
Head length	Eye height	16	1.014 ± 0.110	0.859	1	1.094	11.9	0.925	
Head length	Quadrate height	16	1.188 ± 0.122	0.871	1	1.273	11.8	2.605	$P < 0.025$
Quadrate width	Width b/w eyes	16	0.831 ± 0.044	0.963	1	0.847	11.5	3.341	$P < 0.01$
Quadrate width	Snout height	16	0.634 ± 0.132	0.621	1	0.805	13.0	1.368	
Quadrate width	Eye height	16	0.887 ± 0.121	0.794	1	0.996	12.2	0.038	

Table 19, con't

Quadrate width	Quadrate height	16	0.989 ± 0.162	0.728	1	1.159	12.5	1.099	
Width b/w eyes	Snout height	16	0.802 ± 0.136	0.712	1	0.950	12.5	0.368	
Width b/w eyes	Eye height	16	1.079 ± 0.125	0.841	1	1.177	12.0	1.580	
Width b/w eyes	Quadrate height	16	1.201 ± 0.176	0.769	1	1.369	12.3	2.534	$P < 0.05$
Snout height	Eye height	16	1.072 ± 0.165	0.751	1	1.236	12.4	1.647	
Snout height	Quadrate height	16	1.263 ± 0.185	0.768	1	1.440	12.3	2.933	$P < 0.02$
Eye height	Quadrate height	16	1.134 ± 0.070	0.949	1	1.164	11.5	2.608	$P < 0.025$

Table 20. Scaling relationships of nine log-transformed external morphological variables for preserved specimens of *Crotalus viridis* against log-transformed snout-vent length (SVL). Abbreviations are as in Table 2; see methods (Chapter 5) for complete variable descriptions. $b \pm$ standard error of the mean (s.e.m.), and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against SVL as well as between the sexes from OLS values. Differences from predicted slopes for geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988, $n = N$-2 with $\alpha = 0.05$). * Regressions within each sex were significant after Bonferroni correction.

	N	$b \pm$ s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males								
Tail length	39	1.131 ± 0.055	0.920	1	1.179	27.4	3.595	$P < 0.005$*
Head volume	20	2.216 ± 0.208	0.863	3	2.385	14.7	2.700	$P < 0.025$
1/2 volume	20	2.932 ± 0.182	0.935	3	3.032	14.3	0.182	
1/2 – head volume	20	3.039 ± 0.193	0.932	3	3.146	14.3	0.794	
Total volume	20	2.808 ± 0.186	0.927	3	2.916	14.3	0.459	
1/4 cross-sectional area	21	1.775 ± 0.149	0.882	2	1.890	15.3	0.734	
1/2 cross-sectional area	21	1.774 ± 0.144	0.885	2	1.853	15.3	1.004	
3/4 cross-sectional area	21	1.975 ± 0.172	0.874	2	2.112	15.3	0.688	
Total mass	40	2.843 ± 0.099	0.956	3	2.907	27.7	0.938	
Females								
Tail length	30	0.933 ± 0.050	0.927	1	0.969	21.2	0.631	
Head volume	16	2.062 ± 0.089	0.975	3	2.089	11.4	8.863	$P < 0.001$*
1/2 volume	16	2.772 ± 0.119	0.975	3	2.809	11.4	1.616	
1/2 – head volume	16	2.855 ± 0.130	0.972	3	2.896	11.4	0.820	
Total volume	16	3.016 ± 0.156	0.964	3	3.071	11.5	0.479	

Table 20, con't

1/4 cross-sectional area	16	1.908 ± 0.171	0.898	2	2.013	11.7	0.077	
1/2 cross-sectional area	16	1.873 ± 0.157	0.911	2	1.963	11.7	0.240	
3/4 cross-sectional area	16	2.007 ± 0.185	0.893	2	2.124	11.8	0.711	
Total mass	30	2.963 ± 0.081	0.979	3	2.993	20.8	0.088	

Table 21. Scaling relationships of nine log-transformed external morphological variables for preserved specimens of *Crotalus viridis* against log-transformed total mass. Abbreviations are as in Table 2; see methods (Chapter 5) for complete variable descriptions. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against total mass as well as between the sexes from OLS values. Differences from predicted slopes for geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988, $n = N$-2 with $\alpha = 0.05$). * Regressions within each sex were significant after Bonferroni correction.

	N	$b \pm$ s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males								
Snout-vent length	40	0.336 ± 0.012	0.956	0.333	0.344	27.7	1.199	
Tail length	39	0.376 ± 0.024	0.870	0.333	0.403	27.9	3.417	$P < 0.005$*
Head volume	20	0.789 ± 0.067	0.885	1	0.838	14.6	2.265	$P < 0.05$
1/2 volume	20	1.044 ± 0.042	0.972	1	1.059	14.1	1.489	
1/2 – head volume	20	1.083 ± 0.044	0.971	1	1.099	14.1	2.428	$P < 0.05$
Total volume	20	1.017 ± 0.016	0.995	1	1.019	14.0	1.163	
1/4 cross-sectional area	21	0.630 ± 0.045	0.913	0.667	0.659	15.1	0.023	
1/2 cross-sectional area	21	0.629 ± 0.035	0.943	0.667	0.648	15.0	0.350	
3/4 cross-sectional area	21	0.712 ± 0.044	0.933	0.667	0.737	15.0	1.908	
Females								
Snout-vent length	30	0.330 ± 0.009	0.979	0.333	0.333	20.8	0.373	
Tail length	30	0.309 ± 0.018	0.906	0.333	0.340	21.3	0.521	
Head volume	16	0.684 ± 0.033	0.969	1	0.695	11.5	8.000	$P < 0.001$*
1/2 volume	16	0.932 ± 0.017	0.995	1	0.934	11.4	3.748	$P < 0.005$*
1/2 – head volume	16	0.961 ± 0.018	0.995	1	0.963	11.4	2.069	

Table 21, con't

Total volume	16	1.016 ± 0.028	0.989	1	1.021	11.4	0.771	
1/4 cross-sectional area	16	0.640 ± 0.052	0.915	0.667	0.669	11.7	0.175	
1/2 cross-sectional area	16	0.635 ± 0.040	0.946	0.667	0.653	11.5	0.187	
3/4 cross-sectional area	16	0.683 ± 0.048	0.936	0.667	0.706	11.6	1.038	

Table 22. Scaling relationships of seven log-transformed external morphological variables for preserved specimens of *Crotalus viridis* against log-transformed snout-vent length (SVL) and log-transformed total mass. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against SVL and total mass as well as between the sexes from OLS values. Differences from predicted slopes under geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988; $n = N$-2 with $\alpha = 0.05$). * Regressions for each independent variable within each sex were significant after Bonferroni correction.

	N	$b \pm$ s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males - SVL								
Jaw length	24	0.714 ± 0.023	0.977	1	0.723	16.8	10.270	$P < 0.001$*
Head length	24	0.701 ± 0.024	0.975	1	0.710	16.8	10.380	$P < 0.001$*
Quadrate width	24	0.753 ± 0.033	0.959	1	0.769	16.9	6.216	$P < 0.001$*
Width between eyes	24	0.755 ± 0.052	0.904	1	0.794	17.2	3.572	$P < 0.005$*
Snout height	24	0.692 ± 0.047	0.909	1	0.726	17.2	5.088	$P < 0.001$*
Eye height	24	0.666 ± 0.037	0.938	1	0.688	17.0	7.202	$P < 0.001$*
Quadrate height	24	0.735 ± 0.045	0.925	1	0.764	17.1	4.713	$P < 0.001$*
Males – Total mass								
Jaw length	24	0.243 ± 0.010	0.983	0.333	0.252	16.8	9.984	$P < 0.001$*
Head length	24	0.237 ± 0.011	0.955	0.333	0.243	16.9	6.958	$P < 0.001$*
Quadrate width	24	0.258 ± 0.011	0.961	0.333	0.263	16.9	5.511	$P < 0.001$*
Width between eyes	24	0.260 ± 0.017	0.916	0.333	0.272	17.1	3.218	$P < 0.01$*
Snout height	24	0.232 ± 0.019	0.877	0.333	0.248	17.4	3.914	$P < 0.005$*
Eye height	24	0.228 ± 0.012	0.942	0.333	0.235	17.0	6.777	$P < 0.001$*
Quadrate height	24	0.252 ± 0.015	0.928	0.333	0.262	17.1	4.146	$P < 0.001$*

Table 22, con't

Females - SVL								
Jaw length	18	0.730 ± 0.018	0.991	1	0.734	12.7	13.46	$P < 0.001$*
Head length	18	0.719 ± 0.027	0.978	1	0.727	12.8	8.863	$P < 0.001$*
Quadrate width	18	0.762 ± 0.050	0.936	1	0.788	12.9	3.883	$P < 0.005$*
Width between eyes	18	0.778 ± 0.064	0.902	1	0.819	13.1	2.631	$P < 0.025$*
Snout height	18	0.677 ± 0.051	0.917	1	0.707	13.0	4.969	$P < 0.001$*
Eye height	18	0.624 ± 0.054	0.893	1	0.660	13.1	5.231	$P < 0.001$*
Quadrate height	18	0.726 ± 0.068	0.877	1	0.775	13.2	2.999	$P < 0.025$*
Females – Total mass								
Jaw length	18	0.235 ± 0.005	0.992	0.333	0.236	12.7	15.47	$P < 0.001$*
Head length	18	0.232 ± 0.009	0.978	0.333	0.235	12.8	9.487	$P < 0.001$*
Quadrate width	18	0.246 ± 0.016	0.936	0.333	0.254	12.9	4.258	$P < 0.001$*
Width between eyes	18	0.251 ± 0.020	0.904	0.333	0.264	13.1	2.973	$P < 0.025$*
Snout height	18	0.217 ± 0.018	0.905	0.333	0.228	13.1	4.936	$P < 0.001$*
Eye height	18	0.202 ± 0.017	0.896	0.333	0.213	13.1	5.579	$P < 0.001$*
Quadrate height	18	0.236 ± 0.021	0.891	0.333	0.250	13.1	3.467	$P < 0.005$*

Table 23. Scaling interrelationships of seven log-transformed external cranial morphological variables for preserved specimens of *Crotalus viridis*. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against each cranial measurement as well as between the sexes from OLS values. Differences from predicted slopes under geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988; $n = N$-2 with $\alpha = 0.05$). No regressions were significant after Bonferroni correction.

Independent var.	Dependent var.	*N*	$b \pm$ s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males									
Jaw length	Head length	24	0.977 ± 0.023	0.988	1	0.992	16.7	0.237	
Jaw length	Quadrate width	24	1.033 ± 0.055	0.941	1	1.073	12.9	1.189	
Jaw length	Width b/w eyes	24	1.054 ± 0.066	0.920	1	1.116	13.1	1.388	
Jaw length	Snout height	24	0.966 ± 0.060	0.921	1	0.964	13.1	0.492	
Jaw length	Eye height	24	0.928 ± 0.047	0.947	1	0.901	13.1	1.291	
Jaw length	Quadrate height	24	1.032 ± 0.049	0.952	1	1.057	13.2	0.636	
Head length	Quadrate width	24	1.052 ± 0.055	0.944	1	1.083	17.0	1.624	
Head length	Width b/w eyes	24	1.071 ± 0.069	0.917	1	1.118	17.1	1.856	
Head length	Snout height	24	0.982 ± 0.061	0.921	1	1.023	17.1	0.387	
Head length	Eye height	24	0.938 ± 0.053	0.935	1	0.970	17.0	0.573	
Head length	Quadrate height	24	1.041 ± 0.059	0.935	1	1.077	17.0	1.387	
Quadrate width	Width b/w eyes	24	0.986 ± 0.065	0.913	1	1.032	17.2	0.519	
Quadrate width	Snout height	24	0.890 ± 0.068	0.888	1	0.945	17.3	0.814	
Quadrate width	Eye height	24	0.865 ± 0.049	0.933	1	0.895	17.0	2.046	

Table 23, con't

Quadrate width	Quadrate height	24	0.948 ± 0.063	0.91	1	0.994	17.2	0.101	
Width b/w eyes	Snout height	24	0.825 ± 0.084	0.813	1	0.916	17.8	0.977	
Width b/w eyes	Eye height	24	0.806 ± 0.068	0.863	1	0.868	17.5	1.840	
Width b/w eyes	Quadrate height	24	0.893 ± 0.076	0.861	1	0.962	17.5	0.495	
Snout height	Eye height	24	0.924 ± 0.045	0.951	1	0.948	16.9	1.164	
Snout height	Quadrate height	24	1.015 ± 0.059	0.931	1	1.052	17.1	0.922	
Eye height	Quadrate height	24	1.084 ± 0.051	0.953	1	1.111	16.9	2.322	$P < 0.05$
Females									
Jaw length	Head length	18	0.982 ± 0.035	0.980	1	0.992	12.8	0.237	
Jaw length	Quadrate width	18	1.041 ± 0.066	0.940	1	1.073	12.9	1.189	
Jaw length	Width b/w eyes	18	1.055 ± 0.091	0.893	1	1.116	13.1	1.388	
Jaw length	Snout height	18	0.918 ± 0.074	0.907	1	0.964	13.1	0.492	
Jaw length	Eye height	18	0.850 ± 0.075	0.890	1	0.901	13.1	1.291	
Jaw length	Quadrate height	18	0.987 ± 0.094	0.872	1	1.057	13.2	0.636	
Head length	Quadrate width	18	1.038 ± 0.076	0.921	1	1.082	13.0	1.161	
Head length	Width b/w eyes	18	1.062 ± 0.093	0.910	1	1.125	13.1	1.619	
Head length	Snout height	18	0.930 ± 0.070	0.916	1	0.972	13.0	0.407	
Head length	Eye height	18	0.867 ± 0.068	0.910	1	0.909	13.1	1.314	
Head length	Quadrate height	18	1.010 ± 0.084	0.899	1	1.065	13.1	0.822	
Quadrate width	Width b/w eyes	18	1.021 ± 0.049	0.965	1	1.040	12.8	0.858	
Quadrate width	Snout height	18	0.829 ± 0.086	0.852	1	0.898	13.3	1.151	
Quadrate width	Eye height	18	0.753 ± 0.093	0.804	1	0.839	13.6	1.630	

Table 23, con't

Quadrate width	Quadrate height	18	0.871 ± 0.115	0.782	1	0.985	13.7	0.131	
Width b/w eyes	Snout height	18	0.802 ± 0.080	0.862	1	0.864	13.3	1.620	
Width b/w eyes	Eye height	18	0.733 ± 0.085	0.824	1	0.807	13.5	2.104	
Width b/w eyes	Quadrate height	18	0.845 ± 0.107	0.797	1	0.946	13.6	0.506	
Snout height	Eye height	18	0.917 ± 0.046	0.961	1	0.935	12.8	1.409	
Snout height	Quadrate height	18	1.045 ± 0.082	0.910	1	1.095	13.1	1.252	
Eye height	Quadrate height	18	1.145 ± 0.066	0.950	1	1.172	12.9	2.931	$P < 0.02$

Table 24. Scaling relationships of nine log-transformed external morphological variables for preserved specimens of *Crotalus willardi* against log-transformed snout-vent length (SVL). Abbreviations are as in Table 2; see methods (Chapter 3) for complete variable descriptions. $b \pm$ standard error of the mean (s.e.m.), and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against SVL as well as between the sexes from OLS values. Differences from predicted slopes for geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988, $n = N$-2 with $\alpha = 0.05$). * Regressions within each sex were significant after Bonferroni correction.

	N	$b \pm$ s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males								
Tail length	15	0.911 ± 0.047	0.966	1	0.927	10.8	1.544	
Head volume	16	1.900 ± 0.107	0.958	3	1.941	11.5	8.231	$P < 0.001$*
1/2 volume	12	2.896 ± 0.175	0.965	3	2.949	8.8	0.303	
1/2 – head volume	12	3.024 ± 0.186	0.964	3	3.079	8.8	0.457	
Total volume	12	3.029 ± 0.173	0.968	3	3.078	8.8	0.477	
1/4 cross-sectional area	15	2.087 ± 0.139	0.945	2	2.147	10.9	1.132	
1/2 cross-sectional area	13	2.009 ± 0.121	0.961	2	2.050	9.5	0.433	
3/4 cross-sectional area	15	2.219 ± 0.099	0.975	2	2.248	10.8	2.769	$P < 0.02$
Total mass	15	3.091 ± 0.110	0.984	3	3.116	10.7	1.122	
Females								
Tail length	17	0.861 ± 0.062	0.928	1	0.894	12.3	1.669	
Head volume	17	1.914 ± 0.202	0.857	3	2.067	12.6	3.941	$P < 0.005$*
1/2 volume	13	2.998 ± 0.220	0.944	3	3.084	9.5	0.406	
1/2 – head volume	13	3.147 ± 0.235	0.942	3	3.241	9.5	1.111	
Total volume	13	3.013 ± 0.249	0.93	3	3.126	9.5	0.537	

Table 24, con't

1/4 cross-sectional area	16	1.902 ± 0.173	0.897	2	2.008	11.7	0.051	
1/2 cross-sectional area	15	1.797 ± 0.162	0.904	2	1.890	11.0	0.686	
3/4 cross-sectional area	15	1.992 ± 0.192	0.892	2	2.108	11.0	0.598	
Total mass	15	2.968 ± 0.147	0.969	3	3.016	10.8	1.911	

Table 25. Scaling relationships of nine log-transformed external morphological variables for preserved specimens of *Crotalus willardi* against log-transformed total mass. Abbreviations are as in Table 2; see methods (Chapter 3) for complete variable descriptions. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against total mass as well as between the sexes from OLS values. Differences from predicted slopes for geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988, $n = N$-2 with $\alpha = 0.05$). * Regressions within each sex were significant after Bonferroni correction.

	N	$b \pm$ s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males								
Snout-vent length	15	0.318 ± 0.011	0.984	0.333	0.321	10.7	0.858	
Tail length	14	0.284 ± 0.020	0.944	0.333	0.292	10.2	1.839	
Head volume	15	0.610 ± 0.038	0.952	1	0.625	10.8	8.027	$P < 0.001$*
1/2 volume	12	0.908 ± 0.057	0.962	1	0.926	8.8	1.316	
1/2 – head volume	12	0.948 ± 0.062	0.959	1	0.968	8.8	0.527	
Total volume	12	0.950 ± 0.056	0.967	1	0.966	8.8	0.623	
1/4 cross-sectional area	15	0.670 ± 0.044	0.947	0.667	0.689	10.9	0.689	
1/2 cross-sectional area	13	0.645 ± 0.045	0.949	0.667	0.662	9.5	0.051	
3/4 cross-sectional area	15	0.714 ± 0.029	0.979	0.667	0.721	10.7	2.290	P < 0.05
Females								
Snout-vent length	15	0.327 ± 0.016	0.969	0.333	0.332	10.8	0.149	
Tail length	15	0.291 ± 0.022	0.933	0.333	0.301	10.9	1.318	
Head volume	15	0.660 ± 0.037	0.961	1	0.673	10.8	7.490	$P < 0.001$*
1/2 volume	13	1.006 ± 0.070	0.949	1	1.033	9.5	0.496	
1/2 – head volume	13	1.056 ± 0.076	0.946	1	1.085	9.5	1.220	

Table 25, con’t

Total volume	13	1.010 ± 0.082	0.933	1	1.046	9.5	0.596	
1/4 cross-sectional area	15	0.639 ± 0.047	0.935	0.667	0.661	10.9	0.018	
1/2 cross-sectional area	14	0.610 ± 0.037	0.958	0.667	0.623	10.1	1.013	
3/4 cross-sectional area	14	0.684 ± 0.049	0.941	0.667	0.705	10.2	0.982	

Table 26. Scaling relationships of seven log-transformed external morphological variables for preserved specimens of *Crotalus willardi* against log-transformed snout-vent length (SVL) and log-transformed total mass. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against SVL and total mass as well as between the sexes from OLS values. Differences from predicted slopes under geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988; $n = N$-2 with $\alpha = 0.05$). * Regressions for each independent variable within each sex were significant after Bonferroni correction.

	N	$b \pm$ s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males - SVL								
Jaw length	15	0.635 ± 0.031	0.969	1	0.645	10.8	9.330	*P* < 0.001*
Head length	15	0.673 ± 0.031	0.972	1	0.683	10.8	8.540	*P* < 0.001*
Quadrate width	15	0.764 ± 0.054	0.939	1	0.788	10.9	3.601	*P* < 0.005*
Width between eyes	15	0.690 ± 0.051	0.935	1	0.714	10.9	4.953	*P* < 0.001*
Snout height	14	0.554 ± 0.049	0.914	1	0.579	10.3	6.708	*P* < 0.001*
Eye height	14	0.597 ± 0.045	0.935	1	0.617	10.2	6.820	*P* < 0.001*
Quadrate height	14	0.639 ± 0.051	0.928	1	0.663	10.2	5.525	*P* < 0.001*
Males – Total mass								
Jaw length	14	0.195 ± 0.015	0.938	0.333	0.201	10.2	7.147	*P* < 0.001*
Head length	14	0.207 ± 0.012	0.96	0.333	0.211	10.1	8.043	*P* < 0.001*
Quadrate width	14	0.239 ± 0.019	0.927	0.333	0.248	10.2	3.802	*P* < 0.005*
Width between eyes	14	0.212 ± 0.021	0.895	0.333	0.224	10.4	4.306	*P* < 0.005*
Snout height	13	0.178 ± 0.012	0.953	0.333	0.182	9.5	9.476	*P* < 0.001*
Eye height	13	0.188 ± 0.012	0.957	0.333	0.192	9.5	9.028	*P* < 0.001*

Table 26, con't

Quadrate height	13	0.202 ± 0.014	0.951	0.333	0.207	9.5	7.285	$P < 0.001$*
Females - SVL								
Jaw length	15	0.701 ± 0.038	0.963	1	0.715	10.8	6.537	$P < 0.001$*
Head length	15	0.661 ± 0.038	0.959	1	0.675	10.8	7.258	$P < 0.001$*
Quadrate width	15	0.677 ± 0.050	0.933	1	0.701	10.9	5.139	$P < 0.001$*
Width between eyes	15	0.625 ± 0.048	0.929	1	0.648	10.9	6.085	$P < 0.001$*
Snout height	15	0.653 ± 0.079	0.839	1	0.713	11.3	3.156	$P < 0.025$*
Eye height	15	0.625 ± 0.058	0.900	1	0.659	11.0	4.929	$P < 0.001$*
Quadrate height	15	0.676 ± 0.055	0.920	1	0.705	11.0	4.626	$P < 0.001$*
Females – Total mass								
Jaw length	13	0.230 ± 0.017	0.941	0.333	0.237	9.5	4.714	$P < 0.001$*
Head length	13	0.217 ± 0.018	0.929	0.333	0.225	9.6	4.973	$P < 0.001$*
Quadrate width	13	0.228 ± 0.016	0.948	0.333	0.234	9.5	5.201	$P < 0.001$*
Width between eyes	13	0.214 ± 0.013	0.963	0.333	0.218	9.4	7.455	$P < 0.001$*
Snout height	13	0.215 ± 0.028	0.843	0.333	0.234	9.8	2.998	$P < 0.025$*
Eye height	13	0.211 ± 0.018	0.928	0.333	0.219	9.6	5.287	$P < 0.001$*
Quadrate height	13	0.231 ± 0.012	0.970	0.333	0.235	9.4	6.831	$P < 0.001$*

Table 27. Scaling interrelationships of seven log-transformed external cranial morphological variables for preserved specimens of *Crotalus willardi*. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against each cranial measurement as well as between the sexes from OLS values. Differences from predicted slopes under geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988; $n = N$-2 with $\alpha = 0.05$). No regressions were significant after a Bonferroni correction.

Independent var.	Dependent var.	*N*	$b \pm$ s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males									
Jaw length	Head length	15	1.050 ± 0.037	0.984	1	0.946	10.7	1.258	
Jaw length	Width b/w eyes	15	1.171 ± 0.098	0.916	1	0.981	10.8	0.343	
Jaw length	Eyes width	15	1.068 ± 0.081	0.930	1	0.909	10.9	1.354	
Jaw length	Snout height	14	0.834 ± 0.096	0.863	1	0.999	11.3	0.01	
Jaw length	Eye height	14	0.906 ± 0.088	0.899	1	0.922	11.0	0.983	
Jaw length	Quadrate height	14	0.971 ± 0.097	0.894	1	0.986	11.0	0.174	
Head length	Quadrate width	15	1.113 ± 0.086	0.928	1	1.156	10.9	2.019	
Head length	Width b/w eyes	15	1.002 ± 0.084	0.916	1	1.047	11.0	0.593	
Head length	Snout height	14	0.784 ± 0.093	0.857	1	0.847	10.5	1.587	
Head length	Eye height	14	0.860 ± 0.078	0.909	1	0.901	10.3	1.240	
Head length	Quadrate height	14	0.923 ± 0.086	0.906	1	0.97	10.3	0.364	
Quadrate width	Width b/w eyes	15	0.883 ± 0.055	0.952	1	0.905	10.8	1.710	
Quadrate width	Snout height	14	0.705 ± 0.064	0.911	1	0.739	10.3	3.656	$P < 0.01$
Quadrate width	Eye height	14	0.769 ± 0.046	0.959	1	0.785	10.1	4.299	$P < 0.005$

Table 27, con't

Quadrate width	Quadrate height	14	0.823 ± 0.055	0.949	1	0.845	10.2	2.689	$P < 0.025$
Width b/w eyes	Snout height	14	0.777 ± 0.071	0.91	1	0.814	10.3	2.466	$P < 0.05$
Width b/w eyes	Eye height	14	0.826 ± 0.076	0.907	1	0.868	10.3	1.679	
Width b/w eyes	Quadrate height	14	0.892 ± 0.079	0.915	1	0.933	10.3	0.857	
Snout height	Eye height	14	1.013 ± 0.094	0.906	1	1.064	10.3	0.730	
Snout height	Quadrate height	14	1.098 ± 0.092	0.922	1	1.144	10.3	1.734	
Eye height	Quadrate height	14	1.069 ± 0.034	0.988	1	1.075	10.0	2.394	$P < 0.05$
Females									
Jaw length	Head length	15	0.933 ± 0.043	0.973	1	0.946	10.8	1.258	
Jaw length	Quadrate width	15	0.958 ± 0.058	0.954	1	0.981	10.8	0.343	
Jaw length	Width b/w eyes	15	0.876 ± 0.067	0.930	1	0.909	10.9	1.354	
Jaw length	Snout height	15	0.916 ± 0.110	0.842	1	0.999	11.3	0.010	
Jaw length	Eye height	15	0.877 ± 0.079	0.905	1	0.922	11.0	0.983	
Jaw length	Quadrate height	15	0.943 ± 0.081	0.913	1	0.986	11.0	0.174	
Head length	Quadrate width	15	0.999 ± 0.078	0.927	1	1.037	10.9	0.508	
Head length	Width b/w eyes	15	0.927 ± 0.070	0.931	1	0.961	10.9	0.572	
Head length	Snout height	15	0.952 ± 0.126	0.814	1	1.055	11.4	0.468	
Head length	Eye height	15	0.910 ± 0.097	0.871	1	0.975	11.2	0.260	
Head length	Quadrate height	15	0.977 ± 0.102	0.876	1	1.044	11.1	0.456	
Quadrate width	Width b/w eyes	15	0.901 ± 0.060	0.945	1	0.927	10.9	1.210	
Quadrate width	Snout height	15	0.925 ± 0.118	0.826	1	1.018	11.3	0.157	
Quadrate width	Eye height	15	0.907 ± 0.069	0.931	1	0.94	10.9	0.883	

Table 27, con't

Quadrate width	Quadrate height	15	0.965 ± 0.080	0.919	1	1.007	11.0	0.096	
Width b/w eyes	Snout height	15	0.941 ± 0.157	0.734	1	1.098	11.7	0.678	
Width b/w eyes	Eye height	15	0.948 ± 0.100	0.873	1	1.015	11.1	0.156	
Width b/w eyes	Quadrate height	15	1.042 ± 0.086	0.919	1	1.087	11.0	1.091	
Snout height	Eye height	15	0.873 ± 0.084	0.893	1	0.924	11.1	0.907	
Snout height	Quadrate height	15	0.922 ± 0.099	0.869	1	0.989	11.1	0.112	
Eye height	Quadrate height	15	1.034 ± 0.077	0.934	1	1.070	10.9	0.991	

Table 28. Scaling relationships of nine log-transformed external morphological variables for preserved specimens of *Sistrurus catenatus* against log-transformed snout-vent length (SVL). Abbreviations are as in Table 2; see methods (Chapter 3) for complete variable descriptions. $b \pm$ standard error of the mean (s.e.m.), and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against SVL as well as between the sexes from OLS values. Differences from predicted slopes for geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988, $n = N$-2 with $\alpha = 0.05$). * Regressions within each sex were significant after Bonferroni correction.

	N	$b \pm$ s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males								
Tail length	25	0.963 ± 0.112	0.762	1	1.103	18.8	0.985	
Head volume	13	2.270 ± 0.113	0.773	3	2.582	10.1	1.090	
1/2 volume	15	2.989 ± 0.103	0.897	3	3.156	11.0	0.592	
1/2 – head volume	15	1.936 ± 0.340	0.526	3	2.670	12.7	0.633	
Total volume	15	2.300 ± 0.248	0.682	3	2.784	11.9	0.495	
1/4 cross-sectional area	13	2.087 ± 0.083	0.829	2	2.552	9.9	2.044	
1/2 cross-sectional area	15	2.323 ± 0.091	0.813	2	2.200	11.4	0.828	
3/4 cross-sectional area	15	1.983 ± 1.017	0.497	2	4.479	12.8	4.254	$P < 0.001$*
Total mass	25	2.948 ± 0.151	0.958	3	3.011	17.6	0.089	
Females								
Tail length	20	0.888 ± 0.090	0.843	1	0.967	14.8	0.366	
Head volume	11	2.299 ± 0.128	0.973	3	2.332	8.1	4.850	$P < 0.001$*
1/2 volume	14	2.616 ± 0.312	0.854	3	2.831	10.5	0.547	
1/2 – head volume	14	2.711 ± 0.367	0.820	3	2.996	10.6	0.013	
Total volume	14	2.755 ± 0.229	0.923	3	2.867	10.3	0.590	

Table 28, con't

1/4 cross-sectional area	12	1.930 ± 0.151	0.943	2	1.988	8.8	0.086	
1/2 cross-sectional area	13	1.890 ± 0.137	0.945	2	1.944	9.5	0.416	
3/4 cross-sectional area	14	2.459 ± 0.554	0.621	2	3.121	11.4	2.605	$P < 0.025$
Total mass	20	2.975 ± 0.124	0.970	3	3.020	14.1	0.170	

Table 29. Scaling relationships of nine log-transformed external morphological variables for preserved specimens of *Sistrurus catenatus* against log-transformed total mass. Abbreviations are as in Table 2; see methods (Chapter 3) for complete variable descriptions. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against total mass as well as between the sexes from OLS values. Differences from predicted slopes for geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988, $n = N$-2 with $\alpha = 0.05$). * Regressions within each sex were significant after Bonferroni correction.

	N	*b* ± s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males								
Snout-vent length	25	0.325 ± 0.014	0.958	0.333	0.332	17.6	0.142	
Tail length	25	0.330 ± 0.033	0.811	0.333	0.367	18.5	1.187	
Head volume	13	0.742 ± 0.091	0.859	1	0.800	9.8	2.054	
1/2 volume	15	0.920 ± 0.070	0.931	1	0.953	10.9	0.680	
1/2 – head volume	15	0.555 ± 0.162	0.473	1	0.807	12.9	1.107	
Total volume	15	0.725 ± 0.119	0.742	1	0.842	11.7	1.266	
1/4 cross-sectional area	13	0.755 ± 0.071	0.911	0.667	0.791	9.6	2.096	
1/2 cross-sectional area	15	0.635 ± 0.055	0.912	0.667	0.665	11.0	0.094	
3/4 cross-sectional area	15	1.073 ± 0.229	0.628	0.667	1.355	12.2	4.412	$P < 0.001$*
Females								
Snout-vent length	20	0.326 ± 0.014	0.970	0.333	0.331	14.1	0.073	
Tail length	20	0.297 ± 0.028	0.862	0.333	0.320	14.7	0.359	
Head volume	11	0.770 ± 0.061	0.947	1	0.791	8.1	3.214	$P < 0.025$
1/2 volume	14	0.876 ± 0.095	0.877	1	0.936	10.4	0.681	
1/2 – head volume	14	0.872 ± 0.135	0.776	1	0.990	10.8	0.078	

Table 29, con't

Total volume	14	0.904 ± 0.083	0.909	1	0.949	10.3	0.631	
1/4 cross-sectional area	12	0.655 ± 0.043	0.959	0.667	0.669	8.8	0.223	
1/2 cross-sectional area	13	0.629 ± 0.034	0.969	0.667	0.639	9.4	0.629	
3/4 cross-sectional area	14	0.863 ± 0.163	0.700	0.667	1.032	11.1	2.944	$P < 0.025$

Table 30. Scaling relationships of seven log-transformed external morphological variables for preserved specimens of *Sistrurus catenatus* against log-transformed snout-vent length (SVL) and log-transformed total mass. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against SVL and total mass as well as between the sexes from OLS values. Differences from predicted slopes under geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988; $n = N$-2 with $\alpha = 0.05$). * Regressions for each independent variable within each sex were significant after Bonferroni correction.

	N	$b \pm$ s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males - SVL								
Jaw length	17	0.720 ± 0.068	0.883	1	0.766	12.5	3.118	$P < 0.01$
Head length	19	0.698 ± 0.049	0.922	1	0.727	13.7	4.842	$P < 0.001$*
Quadrate width	19	0.786 ± 0.077	0.859	1	0.848	14.0	1.864	
Width between eyes	19	0.789 ± 0.083	0.843	1	0.859	14.1	1.621	
Snout height	17	0.707 ± 0.133	0.652	1	0.876	13.6	0.897	
Eye height	17	0.625 ± 0.098	0.732	1	0.731	13.2	2.421	$P < 0.05$
Quadrate height	17	0.645 ± 0.108	0.705	1	0.768	13.3	1.945	
Males – Total mass								
Jaw length	17	0.223 ± 0.021	0.882	0.333	0.237	12.5	3.831	$P < 0.005$*
Head length	19	0.223 ± 0.016	0.915	0.333	0.233	13.7	5.064	$P < 0.001$*
Quadrate width	19	0.257 ± 0.021	0.899	0.333	0.271	13.8	2.625	$P < 0.025$
Width between eyes	19	0.253 ± 0.026	0.847	0.333	0.275	14.0	1.978	
Snout height	17	0.226 ± 0.039	0.691	0.333	0.272	13.4	1.392	
Eye height	17	0.198 ± 0.029	0.764	0.333	0.227	13.0	3.097	$P < 0.05$
Quadrate height	17	0.213 ± 0.028	0.795	0.333	0.239	12.9	2.858	$P < 0.02$

Table 30, con't

Females - SVL								
Jaw length	18	0.683 ± 0.034	0.962	1	0.696	12.8	7.658	$P < 0.001$*
Head length	18	0.718 ± 0.079	0.838	1	0.785	13.4	2.484	$P < 0.001$*
Quadrate width	18	0.810 ± 0.071	0.892	1	0.858	13.1	1.921	
Width between eyes	18	0.854 ± 0.070	0.902	1	0.899	13.1	1.403	
Snout height	18	0.628 ± 0.069	0.836	1	0.687	13.4	3.821	$P < 0.01$
Eye height	18	0.645 ± 0.053	0.902	1	0.679	13.1	5.100	$P < 0.001$*
Quadrate height	18	0.711 ± 0.055	0.913	1	0.744	13.0	4.139	$P < 0.01$
Females – Total mass								
Jaw length	18	0.232 ± 0.009	0.978	0.333	0.235	12.8	9.487	$P < 0.001$*
Head length	18	0.242 ± 0.027	0.834	0.333	0.265	13.4	2.218	$P < 0.05$
Quadrate width	18	0.276 ± 0.022	0.911	0.333	0.289	13.1	1.819	
Width between eyes	18	0.293 ± 0.019	0.936	0.333	0.303	12.9	1.408	
Snout height	18	0.211 ± 0.024	0.833	0.333	0.231	13.4	3.594	$P < 0.01$
Eye height	18	0.216 ± 0.019	0.894	0.333	0.229	13.1	4.651	$P < 0.001$*
Quadrate height	18	0.239 ± 0.019	0.904	0.333	0.251	13.1	3.625	$P < 0.01$

Table 31. Scaling interrelationships of seven log-transformed external cranial morphological variables for preserved specimens of *Sistrurus catenatus*. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against each cranial measurement as well as between the sexes from OLS values. Differences from predicted slopes under geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988; $n = N$-2 with $\alpha = 0.05$). No regressions were significant after Bonferroni correction.

Independent var.	Dependent var.	*N*	$b \pm$ s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males									
Jaw length	Head length	17	0.937 ± 0.068	0.926	1	0.974	12.3	0.281	
Jaw length	Quadrate width	17	1.017 ± 0.133	0.795	1	1.140	13.1	1.685	
Jaw length	Width b/w eyes	17	1.063 ± 0.104	0.874	1	1.137	13.0	1.870	
Jaw length	Snout height	17	0.928 ± 0.172	0.659	1	1.143	13.4	1.347	
Jaw length	Eye height	17	0.847 ± 0.114	0.788	1	0.955	13.1	0.608	
Jaw length	Quadrate height	17	0.875 ± 0.126	0.762	1	1.002	13.0	0.036	
Head length	Quadrate width	19	1.096 ± 0.096	0.885	1	1.165	13.9	1.908	
Head length	Width b/w eyes	19	1.074 ± 0.120	0.825	1	1.183	14.2	1.703	
Head length	Snout height	17	0.919 ± 0.188	0.614	1	1.174	13.8	1.031	
Head length	Eye height	17	0.863 ± 0.120	0.776	1	0.980	13.0	0.174	
Head length	Quadrate height	17	0.896 ± 0.130	0.759	1	1.029	13.0	0.231	
Quadrate width	Width b/w eyes	19	0.915 ± 0.106	0.815	1	1.013	14.2	0.130	
Quadrate width	Snout height	17	0.824 ± 0.147	0.676	1	1.002	13.5	0.017	
Quadrate width	Eye height	17	0.812 ± 0.094	0.812	1	0.901	12.8	0.959	

Table 31, con't

Quadrate width	Quadrate height	17	0.775 ± 0.107	0.778	1	0.879	13.0	1.098	
Width b/w eyes	Snout height	17	0.726 ± 0.180	0.521	1	1.006	14.3	0.032	
Width b/w eyes	Eye height	17	0.687 ± 0.125	0.670	1	0.840	13.5	1.215	
Width b/w eyes	Quadrate height	17	0.688 ± 0.142	0.610	1	0.881	13.8	0.812	
Snout height	Eye height	17	0.650 ± 0.135	0.607	1	0.834	13.8	1.155	
Snout height	Quadrate height	17	0.715 ± 0.131	0.660	1	0.876	13.5	0.906	
Eye height	Quadrate height	17	0.956 ± 0.112	0.829	1	1.051	12.7	0.477	
Females									
Jaw length	Head length	18	1.039 ± 0.109	0.851	1	1.127	13.3	1.276	
Jaw length	Quadrate width	18	1.167 ± 0.099	0.897	1	1.232	13.1	2.684	P < 0.02
Jaw length	Width b/w eyes	18	1.238 ± 0.091	0.92	1	1.291	13.0	3.722	P < 0.01
Jaw length	Snout height	18	0.899 ± 0.101	0.833	1	0.985	13.4	0.156	
Jaw length	Eye height	18	0.926 ± 0.076	0.902	1	0.975	13.1	0.337	
Jaw length	Quadrate height	18	1.032 ± 0.069	0.933	1	1.068	13.0	1.053	
Head length	Quadrate width	18	0.977 ± 0.123	0.798	1	1.094	13.6	0.825	
Head length	Width b/w eyes	18	1.026 ± 0.128	0.801	1	1.146	13.6	1.263	
Head length	Snout height	18	0.694 ± 0.133	0.631	1	0.874	14.4	0.914	
Head length	Eye height	18	0.788 ± 0.090	0.828	1	0.866	13.4	1.431	
Head length	Quadrate height	18	0.835 ± 0.112	0.776	1	0.948	13.7	0.467	
Quadrate width	Width b/w eyes	18	0.997 ± 0.080	0.906	1	1.047	13.1	0.621	
Quadrate width	Snout height	18	0.677 ± 0.107	0.716	1	0.800	14.0	1.724	
Quadrate width	Eye height	18	0.737 ± 0.072	0.868	1	0.791	13.2	2.664	P < 0.02

Table 31, con't

Quadrate width	Quadrate height	18	0.793 ± 0.088	0.836	1	0.868	13.4	1.446	
Width b/w eyes	Snout height	18	0.687 ± 0.083	0.81	1	0.763	13.5	2.555	P < 0.05
Width b/w eyes	Eye height	18	0.714 ± 0.062	0.894	1	0.756	13.1	3.550	P < 0.01
Width b/w eyes	Quadrate height	18	0.791 ± 0.061	0.914	1	0.827	13.0	2.664	P < 0.02
Snout height	Eye height	18	0.920 ± 0.091	0.863	1	0.990	13.3	0.108	
Snout height	Quadrate height	18	0.989 ± 0.111	0.832	1	1.084	13.4	0.815	
Eye height	Quadrate height	18	1.041 ± 0.085	0.903	1	1.096	13.1	1.211	

Table 32. Scaling relationships of nine log-transformed external morphological variables for preserved specimens of *Sistrurus miliarius* against log-transformed snout-vent length (SVL). Abbreviations are as in Table 2; see methods (Chapter 3) for complete variable descriptions. $b \pm$ standard error of the mean (s.e.m.), and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against SVL as well as between the sexes from OLS values. Differences from predicted slopes for geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988, $n = N$-2 with $\alpha = 0.05$). * No regressions were significant after Bonferroni correction.

	N	*b* ± s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males								
Tail length	36	1.096 ± 0.048	0.940	1	1.131	25.2	2.975	$P < 0.01$
Head volume	29	1.758 ± 0.252	0.643	3	2.192	22.7	2.779	$P < 0.025$
1/2 volume	31	2.971 ± 0.327	0.739	3	3.455	23.4	1.513	
1/2 – head volume	31	3.089 ± 0.365	0.712	3	3.660	23.6	2.029	
Total volume	31	2.994 ± 0.287	0.790	3	3.368	22.9	1.382	
1/4 cross-sectional area	35	1.850 ± 0.118	0.881	2	1.970	25.0	0.254	
1/2 cross-sectional area	36	1.633 ± 0.186	0.694	2	1.960	27.5	0.214	
3/4 cross-sectional area	36	1.678 ± 0.131	0.828	2	1.844	26.2	1.159	
Total mass	36	2.560 ± 0.113	0.938	3	2.645	25.2	2.996	$P < 0.01$
Females								
Tail length	29	1.102 ± 0.064	0.917	1	1.150	20.6	2.572	$P < 0.025$
Head volume	23	2.420 ± 0.205	0.870	3	2.597	16.7	1.879	
1/2 volume	24	2.891 ± 0.380	0.724	3	3.397	18.4	1.135	
1/2 – head volume	24	2.843 ± 0.609	0.498	3	4.027	20.0	1.993	
Total volume	25	3.039 ± 0.239	0.876	3	3.247	18.1	1.100	

Table 32, con't

1/4 cross-sectional area	27	1.993 ± 0.130	0.905	2	2.096	19.3	0.773	
1/2 cross-sectional area	27	2.068 ± 0.128	0.913	2	2.165	19.2	1.374	
3/4 cross-sectional area	27	2.091 ± 0.137	0.903	2	2.201	19.3	1.568	
Total mass	28	2.930 ± 0.143	0.942	3	3.018	19.7	0.126	

Table 33. Scaling relationships of nine log-transformed external morphological variables for preserved specimens of *Sistrurus miliarius* against log-transformed total mass. Abbreviations are as in Table 2; see methods (Chapter 3) for complete variable descriptions. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against total mass as well as between the sexes from OLS values. Differences from predicted slopes for geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988, $n = N$-2 with $\alpha = 0.05$). * Regressions within each sex were significant after Bonferroni correction.

	N	*b* ± s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males								
Snout-vent length	36	0.366 ± 0.016	0.938	0.333	0.378	25.2	3.233	$P < 0.005$*
Tail length	35	0.399 ± 0.025	0.882	0.333	0.425	25.0	4.291	$P < 0.001$*
Head volume	29	0.593 ± 0.081	0.664	1	0.728	22.5	2.903	$P < 0.01$
1/2 volume	31	0.980 ± 0.079	0.840	1	1.070	22.5	0.925	
1/2 – head volume	31	1.022 ± 0.091	0.813	1	1.133	22.8	1.582	
Total volume	31	1.022 ± 0.038	0.962	1	1.042	21.6	1.150	
1/4 cross-sectional area	35	0.718 ± 0.034	0.932	0.667	0.744	24.6	2.680	$P < 0.025$
1/2 cross-sectional area	36	0.593 ± 0.076	0.640	0.667	0.741	28.0	1.145	
3/4 cross-sectional area	36	0.661 ± 0.038	0.898	0.667	0.697	25.5	1.017	
Females								
Snout-vent length	28	0.321 ± 0.016	0.942	0.333	0.331	19.7	0.038	
Tail length	27	0.359 ± 0.028	0.868	0.333	0.385	19.5	2.170	$P < 0.05$
Head volume	22	0.735 ± 0.063	0.872	1	0.787	16.0	3.069	$P < 0.01$
1/2 volume	23	0.931 ± 0.115	0.758	1	1.069	17.4	0.635	
1/2 – head volume	23	0.908 ± 0.194	0.511	1	1.270	19.1	1.603	

Table 33, con't

Total volume	24	1.011 ± 0.039	0.969	1	1.027	16.8	0.737	
1/4 cross-sectional area	26	0.667 ± 0.037	0.931	0.667	0.691	18.4	0.879	
1/2 cross-sectional area	26	0.700 ± 0.030	0.958	0.667	0.715	18.3	1.953	
3/4 cross-sectional area	26	0.715 ± 0.026	0.969	0.667	0.727	18.2	2.731	$P < 0.025$

Table 34. Scaling relationships of seven log-transformed external morphological variables for preserved specimens of *Sistrurus miliarius* against log-transformed snout-vent length (SVL) and log-transformed total mass. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against SVL and total mass as well as between the sexes from OLS values. Differences from predicted slopes under geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988; $n = N$-2 with $\alpha = 0.05$). * Regressions for each independent variable within each sex were significant after Bonferroni correction.

	N	$b \pm$ s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males - SVL								
Jaw length	17	0.787 ± 0.640	0.911	1	0.825	12.4	2.58	$P < 0.025$
Head length	18	0.605 ± 0.073	0.812	1	0.671	13.5	3.787	$P < 0.005$*
Quadrate width	17	0.642 ± 0.104	0.718	1	0.758	13.2	2.087	
Width between eyes	18	0.702 ± 0.114	0.704	1	0.837	14.1	1.351	
Snout height	17	0.641 ± 0.139	0.587	1	0.837	13.9	1.109	
Eye height	17	0.499 ± 0.121	0.531	1	0.684	14.2	2.214	$P < 0.05$
Quadrate height	17	0.698 ± 0.134	0.644	1	0.869	13.6	0.939	
Males – Total mass								
Jaw length	16	0.242 ± 0.035	0.770	0.333	0.276	12.3	1.454	
Head length	17	0.185 ± 0.033	0.684	0.333	0.224	13.4	2.766	$P < 0.025$
Quadrate width	16	0.199 ± 0.041	0.626	0.333	0.252	12.9	1.718	
Width between eyes	17	0.223 ± 0.048	0.617	0.333	0.285	13.8	0.954	
Snout height	16	0.241 ± 0.044	0.678	0.333	0.293	12.7	0.816	
Eye height	16	0.183 ± 0.041	0.584	0.333	0.240	13.2	1.924	
Quadrate height	16	0.244 ± 0.047	0.661	0.333	0.300	12.8	0.631	

Table 34, con't

Females - SVL								
Jaw length	22	0.678 ± 0.043	0.924	1	0.706	15.7	5.798	$P < 0.001$*
Head length	22	0.660 ± 0.053	0.886	1	0.701	15.9	4.814	$P < 0.001$*
Quadrate width	22	0.715 ± 0.086	0.776	1	0.812	16.6	2.021	
Width between eyes	22	0.650 ± 0.070	0.810	1	0.722	16.4	3.421	$P < 0.005$*
Snout height	22	0.597 ± 0.084	0.714	1	0.707	16.9	2.977	$P < 0.01$*
Eye height	22	0.595 ± 0.062	0.821	1	0.657	16.3	4.554	$P < 0.001$*
Quadrate height	22	0.678 ± 0.071	0.821	1	0.748	16.3	3.140	$P < 0.01$*
Females – Total mass								
Jaw length	20	0.212 ± 0.014	0.930	0.333	0.220	14.3	6.686	$P < 0.001$*
Head length	20	0.202 ± 0.015	0.906	0.333	0.212	14.5	6.279	$P < 0.001$*
Quadrate width	20	0.240 ± 0.023	0.857	0.333	0.259	14.7	2.785	$P < 0.025$*
Width between eyes	20	0.211 ± 0.020	0.865	0.333	0.227	14.7	4.445	$P < 0.001$*
Snout height	20	0.208 ± 0.021	0.849	0.333	0.226	14.7	4.254	$P < 0.001$*
Eye height	20	0.196 ± 0.016	0.888	0.333	0.208	14.5	6.007	$P < 0.001$*
Quadrate height	20	0.219 ± 0.019	0.880	0.333	0.233	14.6	4.354	$P < 0.001$*

Table 35. Scaling interrelationships of seven log-transformed external cranial morphological variables for preserved specimens of *Sistrurus miliarius*. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Reduced major axis (RMA) regressions were determined separately against each cranial measurement as well as between the sexes from OLS values. Differences from predicted slopes under geometric similarity were determined using modified test statistic and degrees of freedom (d.f., rounded to nearest whole integer) from Clarke (1980), with a modification from McArdle (1988; $n = N$-2 with $\alpha = 0.05$). No regressions were significant after Bonferroni correction.

Independent var.	Dependent var.	*N*	$b \pm$ s.e.m.	r^2	Geometric similarity	RMA	d.f.	^{t}observed	significance
Males									
Jaw length	Head length	17	0.873 ± 0.033	0.979	1	0.994	12.1	0.146	
Jaw length	Quadrate width	17	0.794 ± 0.120	0.746	1	1.152	15.9	2.011	
Jaw length	Width b/w eyes	17	0.734 ± 0.144	0.635	1	1.024	16.0	0.321	
Jaw length	Snout height	17	0.709 ± 0.187	0.489	1	1.001	16.6	0.011	
Jaw length	Eye height	17	0.616 ± 0.144	0.551	1	0.931	15.9	0.975	
Jaw length	Quadrate height	17	0.819 ± 0.172	0.603	1	1.061	16.0	0.766	
Head length	Quadrate width	17	0.891 ± 0.140	0.730	1	1.043	13.2	0.326	
Head length	Width b/w eyes	18	0.888 ± 0.219	0.508	1	1.245	15.2	1.29	
Head length	Snout height	17	0.787 ± 0.217	0.468	1	1.151	14.6	0.769	
Head length	Eye height	17	0.648 ± 0.176	0.474	1	0.940	14.6	0.338	
Head length	Quadrate height	17	0.876 ± 0.210	0.536	1	1.197	14.2	1.055	
Quadrate width	Width b/w eyes	17	0.869 ± 0.129	0.752	1	1.002	13.1	0.019	
Quadrate width	Snout height	17	0.682 ± 0.224	0.382	1	1.104	15.1	0.501	
Quadrate width	Eye height	17	0.519 ± 0.191	0.330	1	0.903	15.5	0.501	

Table 35, con't

Quadrate width	Quadrate height	17	0.763 ± 0.221	0.442	1	1.149	14.7	0.744	
Width b/w eyes	Snout height	17	0.651 ± 0.230	0.349	1	1.102	15.3	0.479	
Width b/w eyes	Eye height	17	0.480 ± 0.197	0.283	1	0.902	15.8	0.486	
Width b/w eyes	Quadrate height	17	0.742 ± 0.225	0.420	1	1.145	14.9	0.711	
Snout height	Eye height	17	0.698 ± 0.110	0.728	1	0.818	13.2	1.538	
Snout height	Quadrate height	17	0.954 ± 0.106	0.843	1	1.039	12.7	0.388	
Eye height	Quadrate height	17	1.197 ± 0.110	0.888	1	1.271	12.5	2.863	$P < 0.025$
Females									
Jaw length	Head length	22	0.975 ± 0.043	0.963	1	0.994	15.5	0.146	
Jaw length	Quadrate width	22	1.091 ± 0.083	0.896	1	1.152	15.9	2.011	
Jaw length	Width b/w eyes	22	0.962 ± 0.079	0.881	1	1.024	16.0	0.321	
Jaw length	Snout height	22	0.882 ± 0.106	0.775	1	1.001	16.6	0.011	
Jaw length	Eye height	22	0.877 ± 0.070	0.887	1	0.931	15.9	0.975	
Jaw length	Quadrate height	22	0.993 ± 0.084	0.875	1	1.061	16.0	0.766	
Head length	Quadrate width	22	1.075 ± 0.097	0.860	1	1.160	16.1	1.814	
Head length	Width b/w eyes	22	0.948 ± 0.091	0.846	1	1.030	16.2	0.350	
Head length	Snout height	22	0.821 ± 0.131	0.663	1	1.009	17.3	0.068	
Head length	Eye height	22	0.868 ± 0.079	0.859	1	0.936	16.1	0.803	
Head length	Quadrate height	22	0.989 ± 0.090	0.857	1	1.068	16.1	0.798	
Quadrate width	Width b/w eyes	22	0.850 ± 0.059	0.912	1	0.890	15.8	1.799	
Quadrate width	Snout height	22	0.775 ± 0.088	0.795	1	0.870	16.5	1.412	
Quadrate width	Eye height	22	0.776 ± 0.050	0.922	1	0.808	15.7	3.491	$P < 0.005$

Table 35, con't

Quadrate width	Quadrate height	22	0.855 ± 0.077	0.861	1	0.921	16.1	1.007	
Width b/w eyes	Snout height	22	0.872 ± 0.099	0.796	1	0.978	16.5	0.230	
Width b/w eyes	Eye height	22	0.848 ± 0.073	0.871	1	0.909	16.0	1.219	
Width b/w eyes	Quadrate height	22	0.950 ± 0.092	0.842	1	1.035	16.2	0.395	
Snout height	Eye height	22	0.832 ± 0.093	0.801	1	0.930	16.4	0.750	
Snout height	Quadrate height	22	0.951 ± 0.105	0.805	1	1.060	16.4	0.607	
Eye height	Quadrate height	22	1.109 ± 0.058	0.947	1	1.140	15.6	2.604	$P < 0.025$

Table 36. Raw morphology for adult specimens used in morphological analyses. Only values for adults ≥ minimum reproductive SVL (from literature; see Methods for citations) for given species list. Values are mean ± standard error of the mean. See methods (Chapter 5) for complete description of morphological variables.

	SVL max.-min. (mm)	N	Snout-vent length (mm)	Tail length (mm)	Head volume (ml)	Half volume (ml)	Total volume (ml)
Male							
Crotalus atrox	652 – 1102	18	776.1 ± 22.4	70.9 ± 2.5	16.9 ± 2.2	191.5 ± 25.5	470.1 ± 62.4
Crotalus lepidus	415 – 640	21	516.4 ± 12.9	47.9 ± 1.6	4.2 ± 0.3	59.0 ± 5.8	134.7 ± 11.2
Crotalus viridis	510 – 1010	30	699.1 ± 23.6	58.3 ± 2.2	8.1 ± 1.1	104.7 ± 15.1	231.8 ± 34.0
Crotalus willardi	408 – 595	11	490.7 ± 14.2	61.9 ± 1.0	4.9 ± 0.2	70.8 ± 9.3	160.4 ± 21.4
Sistrurus catenatus	288 – 560	22	381.9 ± 16.6	48.1 ± 2.6	3.2 ± 0.4	43.2 ± 6.2	78.2 ± 10.5
Sistrurus miliarius	350 – 450	6	389.3 ± 18.0	60.5 ± 5.4	1.7 ± 0.3	34.2 ± 6.9	73.4 ± 16.7
Female							
Crotalus atrox	662 – 909	13	755.4 ± 22.3	51.6 ± 1.9	11.9 ± 1.3	139.3 ± 12.5	371.9 ± 36.3
Crotalus lepidus	398 – 465	9	437.2 ± 9.3	33.0 ± 1.2	3.5 ± 0.3	31.5 ± 1.8	80.4 ± 5.6
Crotalus viridis	522 – 796	15	694.1 ± 21.3	42.3 ± 1.2	8.0 ± 0.8	113.3 ± 14.5	261.4 ± 38.4
Crotalus willardi	405 – 510	11	458.5 ± 8.6	47.6 ± 1.4	4.5 ± 0.2	58.3 ± 4.4	120.3 ± 9.6
Sistrurus catenatus	330 – 618	11	476.3 ± 32.0	46.6 ± 3.8	4.1 ± 0.9	66.1 ± 13.5	138.7 ± 31.2
Sistrurus miliarius	380 – 500	3	434.0 ± 35.2	67.0 ± 7.0	3.4 ± 0.9	49.3 ± 9.8	111.1 ± 34.0

Table 37. Raw morphology for adult specimens used in morphological analyses. Only values for adults ≥ minimum reproductive SVL (from literature; see methods [Chapter 5] for citations) for given species list. Values are mean ± standard error of the mean. See methods (Chapter 5) for complete description of morphological variables. Sample size in parentheses if different than listed column.

	N	Cross-sectional area at 25% SVL (mm^2)	Cross-sectional area at 50% SVL (mm^2)	Cross-sectional area at 75% SVL (mm^2)	Body weight (g)	Jaw length (mm)
Male						
Crotalus atrox	18	616.6 ± 70.6	1090.9 ± 113.8	811.1 ± 83.9	446.2 ± 58.2	40.6 ± 1.0
Crotalus lepidus	21	241.4 ± 19.5	395.9 ± 23.8	301.0 ± 13.9	117.8 ± 8.5	24.9 ± 0.6 (15)
Crotalus viridis	30	322.7 ± 28.9	595.7 ± 55.2	471.5 ± 47.1	306.8 ± 32.1	36.0 ± 1.2 (18)
Crotalus willardi	11	347.3 ± 34.6	543.0 ± 35.9	500.6 ± 51.9	162.0 ± 17.2	27.6 ± 0.5
Sistrurus catenatus	22	196.8 ± 23.4	382.7 ± 45.1	281.7 ± 29.1	66.2 ± 9.9	21.8 ± 0.8 (16)
Sistrurus miliarius	6	181.5 ± 38.1	235.7 ± 40.6	209.2 ± 25.0	67.3 ± 14.7	25.3 (1)
Female						
Crotalus atrox	13	458.2 ± 49.5	920.2 ± 101.3	675.0 ± 58.7	360.3 ± 37.3	37.7 ± 1.0
Crotalus lepidus	9	183.5 ± 16.6	335.8 ± 23.0	272.3 ± 14.7	72.6 ± 6.8	22.8 ± 0.3 (6)
Crotalus viridis	15	336.1 ± 31.4	570.3 ± 72.8	458.5 ± 61.9	262.7 ± 24.2	34.4 ± 1.2 (9)
Crotalus willardi	11	207.1 ± 15.5	401.5 ± 29.1	303.2 ± 22.7	100.0 ± 7.5	26.6 ± 0.2 (9)
Sistrurus catenatus	11	266.7 ± 47.4	474.3 ± 70.2	361.9 ± 59.8	124.6 ± 25.1	28.4 ± 3.2 (10)
Sistrurus miliarius	3	236.7 ± 55.3	486.6 ± 115.0	396.8 ± 69.9	121.9 ± 28.7	24.6 ± 0.4

Table 38. Scaling interrelationships of nine log-transformed morphological variables for preserved specimens from six species of rattlesnakes regressed against snout-vent length using non-calibrated values (no independent contrasts). $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and differences from slopes predicted under geometric similarity (GS) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. * Regressions within each sex were significant after Bonferroni correction.

				Slope dif. than zero?			Slope dif. than isometry?		
	N	$b \pm$ s.e.m.	r^2	^{t}observed	significance	GS	^{t}observed	significance	RMA
Males									
Tail length	6	0.292 ± 0.217	0.312	1.346	n. s.	1	3.263	$P < 0.05$	0.523
Head volume	6	2.517 ± 0.472	0.877	5.332	$P < 0.005$*	3	1.023	n. s.	2.689
Half body volume	6	2.042 ± 0.300	0.920	6.803	$P < 0.005$*	3	3.193	$P < 0.05$	2.129
Total body volume	6	2.301 ± 0.307	0.934	7.498	$P < 0.005$*	3	2.277	n. s.	2.382
Cross-sectional area at 25% SVL	6	1.348 ± 0.370	0.769	3.646	$P < 0.02$	2	1.762	n. s.	1.537
Cross-sectional area at 50% SVL	6	1.540 ± 0.424	0.767	3.629	$P < 0.02$	2	1.085	n. s.	1.758
Cross-sectional area at 75% SVL	6	1.435 ± 0.423	0.742	3.390	$P < 0.05$	2	1.336	n. s.	1.667
Total mass	6	2.626 ± 0.251	0.965	10.445	$P < 0.005$*	3	1.490	n. s.	2.674
Jaw length	6	0.769 ± 0.134	0.892	5.748	$P < 0.005$*	1	1.724	n. s.	0.815
Females									
Tail length	6	0.003 ± 0.469	0.001	0.007	n. s.	1	2.126	n. s.	1.000
Head volume	6	2.006 ± 0.195	0.963	10.276	$P < 0.005$*	3	5.098	$P < 0.01$	2.043
Half body volume	6	2.046 ± 0.410	0.861	4.987	$P < 0.005$*	3	2.327	n. s.	2.205
Total body volume	6	2.252 ± 0.281	0.941	8.007	$P < 0.005$*	3	2.662	n. s.	2.322

Table 38, con't

Cross-sectional area at 25% SVL	6	1.257 ± 0.252	0.861	4.987	$P < 0.005$*	2	2.948	$P < 0.05$	1.355
Cross-sectional area at 50% SVL	6	1.207 ± 0.350	0.748	3.443	$P < 0.05$	2	2.266	n. s.	1.395
Cross-sectional area at 75% SVL	6	1.177 ± 0.287	0.808	4.100	$P < 0.01$	2	2.868	$P < 0.05$	1.309
Total mass	6	2.344 ± 0.359	0.914	6.521	$P < 0.005$*	3	1.827	n. s.	2.452
Jaw length	6	0.756 ± 0.106	0.927	7.149	$P < 0.005$*	1	2.301	n. s.	0.785

Table 39. Scaling interrelationships of nine log-transformed morphological variables for preserved specimens from six species of rattlesnakes regressed against total mass using non-calibrated values (no independent contrasts). $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and differences from slopes predicted under geometric similarity (GS) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. * Regressions within each sex were significant after Bonferroni correction.

				Slope diff. than zero?			Slope diff. than isometry?		
	N	$b \pm$ s.e.m.	r^2	^{t}observed	significance	GS	^{t}observed	significance	RMA
Males									
Snout-vent length	6	0.367 ± 0.035	0.965	10.445	$P < 0.005$*	0.333	0.971	n. s.	0.374
Tail length	6	0.128 ± 0.074	0.429	1.733	n. s.	0.333	2.770	n. s.	0.195
Head volume	6	0.957 ± 0.154	0.906	6.193	$P < 0.005$*	1	0.279	n. s.	1.005
Half body volume	6	0.779 ± 0.082	0.957	9.457	$P < 0.005$*	1	2.695	n. s.	0.797
Total body volume	6	0.875 ± 0.082	0.966	10.646	$P < 0.005$*	1	1.524	n. s.	0.890
Cross-sectional area at 25% SVL	6	0.536 ± 0.103	0.870	5.182	$P < 0.005$*	0.667	1.262	n. s.	0.574
Cross-sectional area at 50% SVL	6	0.605 ± 0.129	0.846	4.694	$P < 0.005$*	0.667	0.473	n. s.	0.658
Cross-sectional area at 75% SVL	6	0.579 ± 0.115	0.863	5.020	$P < 0.005$*	0.667	0.756	n. s.	0.623
Jaw length	6	0.292 ± 0.043	0.919	6.758	$P < 0.005$*	0.333	0.954	n. s.	0.304
Females									
Snout-vent length	6	0.390 ± 0.060	0.914	6.521	$P < 0.005$*	0.333	0.950	n. s.	0.408
Tail length	6	0.109 ± 0.183	0.082	0.596	n. s.	0.333	1.224	n. s.	0.381
Head volume	6	0.782 ± 0.145	0.880	5.408	$P < 0.005$*	1	1.403	n. s.	0.834
Half body volume	6	0.869 ± 0.116	0.934	7.522	$P < 0.005$*	1	1.129	n. s.	0.900

Table 39, con't

Total body volume	6	0.935 ± 0.074	0.976	12.717	$P < 0.005$*	1	0.878	n. s.	0.946
Cross-sectional area at 25% SVL	6	0.542 ± 0.052	0.964	10.336	$P < 0.005$*	0.667	2.385	n. s.	0.552
Cross-sectional area at 50% SVL	6	0.542 ± 0.087	0.906	6.225	$P < 0.005$*	0.667	1.425	n. s.	0.569
Cross-sectional area at 75% SVL	6	0.518 ± 0.065	0.942	8.030	$P < 0.005$*	0.667	2.277	n. s.	0.534
Jaw length	6	0.309 ± 0.042	0.932	7.431	$P < 0.005$*	0.333	0.571	n. s.	0.320

Table 40. Scaling interrelationships of nine log-transformed morphological variables for preserved specimens from six species of rattlesnakes regressed against snout-vent length using independent contrasts. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and differences from slopes predicted under geometric similarity (GS) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. * Regressions within each sex were significant after Bonferroni correction.

				Slope dif. than zero?			Slope dif. than isometry?		
	N	$b \pm$ s.e.m.	r^2	^{t}observed	significance	GS	^{t}observed	significance	RMA
Males									
Tail length	5	0.359 ± 0.305	0.258	1.178	n. s.	1	2.102	n. s.	0.707
Head volume	5	2.462 ± 0.701	0.755	3.511	n. s.	3	0.768	n. s.	2.833
Half body volume	5	2.064 ± 0.430	0.852	4.801	$P < 0.01$	3	2.176	n. s.	2.236
Total body volume	5	2.128 ± 0.411	0.870	5.177	$P < 0.01$	3	2.122	n. s.	2.281
Cross-sectional area at 25% SVL	5	1.167 ± 0.423	0.655	2.758	n. s.	2	1.969	n. s.	1.441
Cross-sectional area at 50% SVL	5	1.449 ± 0.595	0.597	2.437	n. s.	2	0.926	n. s.	1.875
Cross-sectional area at 75% SVL	5	1.256 ± 0.560	0.557	2.243	n. s.	2	1.329	n. s.	1.684
Total mass	5	2.615 ± 0.360	0.930	7.263	$P < 0.005$*	3	1.069	n. s.	2.713
Jaw length	5	0.910 ± 0.182	0.862	4.992	$P < 0.01$	1	0.494	n. s.	0.981
Females									
Tail length	5	0.223 ± 0.421	0.066	0.531	n. s.	1	1.846	n. s.	0.868
Head volume	5	1.874 ± 0.159	0.972	11.817	$P < 0.005$*	3	7.082	$P < 0.05$	1.901
Half body volume	5	2.262 ± 0.415	0.881	5.452	$P < 0.005$*	3	1.778	n. s.	2.409
Total body volume	5	2.408 ± 0.202	0.973	11.898	$P < 0.005$*	3	2.931	n. s.	2.442
Cross-sectional area at 25% SVL	5	1.379 ± 0.186	0.932	7.417	$P < 0.005$*	2	3.339	$P < 0.05$	1.428

Table 40, con't

Cross-sectional area at 50% SVL	5	1.291 ± 0.232	0.885	5.555	$P < 0.05$	2	3.056	n. s.	1.372
Cross-sectional area at 75% SVL	5	1.291 ± 0.205	0.909	6.308	$P < 0.005$*	2	3.458	$P < 0.05$	1.355
Total mass	5	2.602 ± 0.277	0.957	9.383	$P < 0.005$*	3	1.437	n. s.	2.661
Jaw length	5	0.786 ± 0.090	0.951	8.786	$P < 0.005$*	1	2.378	n. s.	0.806

Table 41. Scaling interrelationships of nine log-transformed morphological variables for preserved specimens from six species of rattlesnakes regressed against total body mass using independent contrasts. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and differences from slopes predicted under geometric similarity (GS) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. * Regressions within each sex were significant after Bonferroni correction.

				Slope dif. than zero?			Slope dif. than isometry?		
	N	$b \pm$ s.e.m.	r^2	^{t}observed	significance	GS	^{t}observed	significance	RMA
Males									
Snout-vent length	5	0.355 ± 0.049	0.930	7.263	$P < 0.005$*	0.333	0.449	n. s.	0.368
Tail length	5	0.164 ± 0.101	0.395	1.615	n. s.	0.333	1.673	n. s.	0.261
Head volume	5	0.927 ± 0.241	0.788	3.852	$P < 0.02$	1	0.303	n. s.	1.044
Half body volume	5	0.786 ± 0.125	0.909	6.306	$P < 0.005$*	1	1.712	n. s.	0.825
Total body volume	5	0.805 ± 0.122	0.916	6.600	$P < 0.005$*	1	1.598	n. s.	0.841
Cross-sectional area at 25% SVL	5	0.483 ± 0.111	0.825	4.345	$P < 0.02$	0.667	1.649	n. s.	0.532
Cross-sectional area at 50% SVL	5	0.573 ± 0.193	0.688	2.971	$P < 0.05$	0.667	0.482	n. s.	0.690
Cross-sectional area at 75% SVL	5	0.537 ± 0.156	0.748	3.444	$P < 0.05$	0.667	0.827	n. s.	0.621
Jaw length	5	0.347 ± 0.051	0.920	6.777	$P < 0.005$*	0.333	0.274	n. s.	0.362
Females									
Snout-vent length	5	0.368 ± 0.039	0.957	9.383	$P < 0.005$*	0.333	0.897	n. s.	0.376
Tail length	5	0.141 ± 0.148	0.187	0.958	n. s.	0.333	1.297	n. s.	0.326
Head volume	5	0.691 ± 0.090	0.937	7.692	$P < 0.005$*	1	3.433	n. s.	0.714
Half body volume	5	0.861 ± 0.140	0.905	6.161	$P < 0.005$*	1	0.993	n. s.	0.905
Total body volume	5	0.901 ± 0.087	0.964	10.402	$P < 0.001$*	1	1.138	n. s.	0.918

Table 41, con't

Cross-sectional area at 25% SVL	5	0.524 ± 0.058	0.953	9.025	$P < 0.001$*	0.667	2.448	n. s.	0.537
Cross-sectional area at 50% SVL	5	0.499 ± 0.065	0.937	7.704	$P < 0.005$*	0.667	2.569	n. s.	0.515
Cross-sectional area at 75% SVL	5	0.497 ± 0.056	0.951	8.821	$P < 0.001$*	0.667	3.018	n. s.	0.510
Jaw length	5	0.292 ± 0.040	0.929	7.228	$P < 0.005$*	0.333	1.025	n. s.	0.303

Table 42. Raw kinematic data for adult snakes from six species of rattlesnakes used in feeding strike analyses: mass, snout-vent length (SVL), tail length (TL), # strikes, maximal velocity, maximal acceleration, distance of strike. See methods (Chapter 5) for complete variable descriptions. Table entries include mean ± 1 standard deviation (range below).

	# of individuals	Mass (g)	SVL (mm)	# of strikes	Maximal velocity (m/s)	Maximal acceleration (m/s^2)	Strike distance (mm)
Crotalus atrox	6	303.4 ± 98.6 (181.4-439.0)	783.1 ± 65.5 (698.0-855.0)	26	2.141 ± 0.870 (0.823-3.627)	154.146 ± 54.305 (76.666-298.900)	43.22 ± 32.69 (13.00-191.15)
Crotalus lepidus	2	230.5 ± 76.1 (161.0-300.0)	601.5 ± 94.7 (515.0-688.0)	6	2.456 ± 0.995 (1.254-2.596)	193.438 ± 86.893 (83.232-297.757)	44.76 ± 22.52 (11.99-71.57)
Crotalus viridis	4	186.2 ± 44.3 (130.0-232.0)	656.2 ± 95.5 (534.0-771.0)	18	2.156 ± 0.728 (1.001-3.903)	220.894 ± 90.215 (111.512-411.001)	66.57 ± 35.22 (20.90-160.91)
Crotalus willardi	4	104.4 ± 11.9 (86.0-117.0))	448.1 ± 26.2 (410.0-470.0)	14	1.884 ± 0.365 (1.117-2.444)	152.189 ± 12.680 (142.416-173.433)	51.28 ± 48.86 (5.76-114.22)
Sistrurus catenatus	2	119.0 ± 24.1 (97.0-141.0)	486.0 ± 21.1 (464.0-508.0)	6	1.363 ± 0.456 (0.885-1.859)	152.739 ± 25.882 (110.151-186.156)	27.00 ± 17.50 (8.00-58.30)
Sistrurus miliarius	1	268.0	631.0	5	2.156 ± 0.194 (1.823-2.318)	166.286 ± 79.436 (72.779-273.691)	71.37 ± 27.81 (36.80-106.98)

Table 43. Raw kinematic data for adult snakes from six species of rattlesnakes used in feeding strike analyses: maximum gape, time to maximum gape, time interval between maximum gape and initial contact, time to lower jaw contact, time to upper jaw contact, percentage of body kinematically active during strike. See methods (Chapter 5) for complete variable descriptions. Table entries include mean ± 1 standard deviation (range below).

	Maximum gape (degrees)	Time to maximum gape (msec)	Interval between gape and contact (msec)	Time to lower contact (msec)	Time to upper contact (msec)	Percentage of body moving during strike
Crotalus atrox	60.68 ± 11.64 (37.69-79.43)	60.8 ± 26.9 (17.0-119.0)	4.0 ± 4.0 (1.0-12.0)	64.6 ± 26.9 (18.0-120.0)	76.5 ± 27.2 (29.0-141.0)	36.26 ± 6.75 (21.46-49.47)
Crotalus lepidus	52.09 ± 11.65 (35.67-71.49)	45.2 ± 28.8 (23.0-102.0)	9.0 ± 5.0 (4.0-16.0)	55.5 ± 32.5 (29.0-120.0)	61.5 ± 36.5 (32.0-134.0)	43.52 ± 8.38 (29.10-43.71)
Crotalus viridis	62.67 ± 10.93 (44.55-81.07)	57.2 ± 17.0 (36.0-84.0)	5.0 ± 4.0 (1.0-13.0)	67.9 ± 24.8 (39.0-134.0)	75.3 ± 23.0 (48.0-139.0)	38.97 ± 10.19 (24.23-63.99)
Crotalus willardi	54.05 ± 14.41 (31.33-84.05)	54.2 ± 26.3 (21.0-110.0)	5.0 ± 4.0 (1.0-14.0)	54.6 ± 26.1 (21.0-110.0)	58.4 ± 26.9 (25.0-114.0)	40.34 ± 8.66 (28.24-55.07)
Sistrurus catenatus	55.42 ± 21.19 (35.81-82.39)	41.8 ± 17.0 (24.0-69.0)	3.0 ± 2.0 (1.0-6.0)	41.8 ± 17.0 (24.0-69.0)	53.5 ± 12.8 (36.0-72.0)	35.67 ± 7.80 (22.23-43.78)
Sistrurus miliarius	53.34 ± 6.31 (45.60-62.94)	69.8 ± 21.5 (34.0-89.0)	6.0 ± 5.0 (1.0-14.0)	75.0 ± 22.9 (37.0-94.0)	81.2 ± 21.8 (45.0-103.0)	43.09 ± 9.23 (38.03-56.92)

Table 44. Correlated pairs of strike variables taken from product-moment correlations between values for six species of rattlesnakes for seven kinematic variables: maximum velocity, maximum acceleration, strike distance, time to lower jaw contact, time to upper jaw contact, time to maximum gape, % body moving during strike. *Significant after Bonferroni correction.

		F-value	*P*-value
Maximal velocity	Strike distance	55.401	< 0.001*
	Time to lower jaw contact	17.082	< 0.001*
	Time to maximum gape	11.938	0.001*
Strike distance	Time to lower jaw contact	71.614	< 0.001*
	Time to maximum gape	54.079	< 0.001*
	Time interval gape-contact	13.088	< 0.001*
	% body moving during strike	9.422	0.003
Time to lower jaw contact	Time to maximum gape	1702.527	< 0.001*
	Time interval gape-contact	6.508	< 0.001*

Table 45. Scaling interrelationships of maximal acceleration regressed against body mass. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and slope differences from isometry (-0.333) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. No regressions were significant after Bonferroni correction.

				Slope dif. than zero?		Slope dif. than isometry?	
Data partition	*N*	$b \pm$ s.e.m.	r^2	^{t}observed	significance	^{t}observed	significance
Multiple strikes per species							
Multiple strikes per individual	75	-0.113 ± 0.102	0.017	-1.110	n. s.	2.157	$P < 0.05$
Single value per individual	18	-0.144 ± 0.161	0.048	-0.900	n. s.	1.174	n. s.
Non-calibrated species values							
Single best value	6	-0.336 ± 0.331	0.205	-1.020	n. s.	0.009	n. s.
Mean value	6	0.046 ± 0.093	0.058	0.495	n. s.	4.043	$P < 0.02$
Mean value from each individual best value	6	0.013 ± 0.317	0.001	0.042	n. s.	1.082	n. s.
Independent contrasts							
Single best value	5	-0.155 ± 0.285	0.069	-0.540	n. s.	0.625	n. s.
Mean value	5	0.082 ± 0.084	0.190	0.097	n. s.	4.905	$P < 0.02$
Mean value from each individual best value	5	0.028 ± 0.266	0.003	0.105	n. s.	1.346	n. s.

Table 46. Scaling interrelationships of maximal acceleration regressed against snout-vent length. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and slope differences from isometry (-1.0) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. * Regressions were significant after Bonferroni correction.

				Slope dif. than zero?		Slope dif. than isometry?	
Data partition	*N*	$b \pm$ s.e.m.	r^2	^{t}observed	significance	^{t}observed	significance
Multiple strikes per species							
Multiple strikes per individual	75	-0.250 ± 0.206	0.020	-1.210	n. s.	3.641	$P < 0.001$*
Single value per individual	18	-0.299 ± 0.225	0.050	-0.920	n. s.	2.164	$P < 0.05$
Non-calibrated species values							
Single best value	6	-0.541 ± 0.867	0.089	-0.630	n. s.	0.529	n. s.
Mean value	6	-0.019 ± 0.205	0.002	-0.090	n. s.	4.785	$P < 0.01$
Mean value from each individual best value	6	0.027 ± 0.675	0.001	0.039	n. s.	1.521	n. s.
Independent contrasts							
Single best value	5	-0.311 ± 0.669	0.051	-0.47	n. s.	1.030	n. s.
Mean value	5	0.047 ± 0.209	0.013	0.225	n. s.	5.010	$P < 0.02$
Mean value from each individual best value	5	-0.106 ± 0.597	0.008	-0.180	n. s.	1.497	n. s.

Table 47. Scaling interrelationships of maximal velocity regressed against body weight. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and slope differences from isometry (0) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. No regressions were significant after Bonferroni correction.

				Slope dif. than zero?		Slope dif. than isometry?	
Data partition	*N*	$b \pm$ s.e.m.	r^2	$t_{observed}$	significance	$t_{observed}$	significance
Multiple strikes per species							
Multiple strikes per individual	75	0.112 ± 0.093	0.019	1.204	n. s.	1.204	n. s.
Single value per individual	18	0.401 ± 0.142	0.333	2.829	$P < 0.02$	2.824	$P < 0.02$
Non-calibrated species values							
Single best value	6	0.337 ± 0.189	0.444	1.785	n. s.	1.783	n. s.
Mean value	6	0.313 ± 0.370	0.151	0.844	n. s.	0.846	n. s.
Mean value from each individual best value	6	0.500 ± 0.245	0.509	2.036	n. s.	2.041	n. s.
Independent contrasts							
Single best value	5	0.229 ± 0.098	0.576	2.331	n. s.	2.337	n. s.
Mean value	5	0.364 ± 0.353	0.210	1.031	n. s.	1.031	n. s.
Mean value from each individual best value	5	0.452 ± 0.141	0.719	3.200	$P < 0.05$	3.206	$P < 0.05$

Table 48. Scaling interrelationships of maximal velocity regressed against snout-vent length. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and slope differences from isometry (0) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. No regressions were significant after Bonferroni correction.

				Slope dif. than zero?		Slope dif. than isometry?	
Data partition	*N*	$b \pm$ s.e.m.	r^2	^{t}observed	significance	^{t}observed	significance
Multiple strikes per species							
Multiple strikes per individual	75	0.208 ± 0.190	0.016	1.096	n. s.	1.095	n. s.
Single value per individual	18	0.795 ± 0.288	0.322	2.758	$P < 0.02$	2.076	$P < 0.02$
Non-calibrated species values							
Single best value	6	0.939 ± 0.371	0.615	2.529	n. s.	2.531	n. s.
Mean value	6	0.590 ± 0.804	0.119	0.734	n. s.	0.734	n. s.
Mean value from each individual best value	6	1.018 ± 0.546	0.465	1.866	n. s.	1.864	n. s.
Independent contrasts							
Single best value	5	0.646 ± 0.204	0.715	3.164	$P < 0.05$	3.167	n. s.
Mean value	5	0.635 ± 0.833	0.127	0.763	n. s.	0.762	n. s.
Mean value from each individual best value	5	0.847 ± 0.424	0.5	2.000	n. s.	1.998	n. s.

Table 49. Scaling interrelationships of distance regressed against body weight. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and slope differences from isometry (0.333) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. * Regressions were significant after Bonferroni correction.

				Slope dif. than zero?		Slope dif. than isometry?	
Data partition	*N*	$b \pm$ s.e.m.	r^2	^{t}observed	significance	^{t}observed	significance
Multiple strikes per species							
Multiple strikes per individual	75	0.338 ± 0.171	0.051	1.978	n. s.	0.029	n. s.
Single value per individual (acceleration dataset)	18	1.338 ± 0.228	0.683	5.874	P < 0.001*	4.408	*P* < 0.001*
Single value per individual (velocity dataset)	18	0.823 ± 0.228	0.337	2.854	P < 0.02	1.701	n. s.
Non-calibrated species values							
Single best value (acceleration dataset)	6	1.189 ± 0.331	0.764	3.594	P < 0.05	2.586	n. s.
Single best value (velocity dataset)	6	0.619 ± 0.308	0.503	2.013	n. s.	0.929	n. s.
Mean value	6	0.023 ± 0.010	0.115	0.200	n. s.	2.696	n. s.
Independent contrasts							
Single best value (acceleration dataset)	5	1.361 ± 0.277	0.858	4.917	P < 0.01	3.711	P < 0.05
Single best value (velocity dataset)	5	0.526 ± 0.296	0.440	1.773	n. s.	0.652	n. s.
Mean value	5	0.028 ± 0.096	0.021	0.293	n. s.	3.177	n. s.

Table 50. Scaling interrelationships of distance regressed against snout-vent length. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and slope differences from isometry (1.0) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. * Regressions were significant after Bonferroni correction.

				Slope dif. than zero?		Slope dif. than isometry?	
Data partition	*N*	$b \pm$ s.e.m.	r^2	^{t}observed	significance	^{t}observed	significance
Multiple strikes per species							
Multiple strikes per individual	75	0.778 ± 0.344	0.065	2.261	$P < 0.05$	0.645	n. s.
Single value per individual (acceleration dataset)	18	2.634 ± 0.483	0.650	5.456	P < 0.001*	3.383	$P < 0.01$
Single value per individual (velocity dataset)	18	1.867 ± 0.541	0.427	3.452	P < 0.005	1.603	n. s.
Non-calibrated species values							
Single best value (acceleration dataset)	6	2.797 ± 0.903	0.706	3.099	$P < 0.05$	1.990	n. s.
Single best value (velocity dataset)	6	1.842 ± 0.468	0.795	3.936	$P < 0.02$	1.799	n. s.
Mean value	6	-0.063 ± 0.244	0.016	-0.260	n. s.	4.357	$P < 0.02$
Independent contrasts							
Single best value (acceleration dataset)	5	3.082 ± 0.737	0.814	4.181	$P < 0.02$	2.825	n. s.
Single best value (velocity dataset)	5	1.743 ± 0.497	0.755	3.509	$P < 0.05$	1.495	n. s.
Mean value	5	-0.071 ± 0.214	0.026	-0.330	n. s.	5.005	$P < 0.02$

Table 51. Scaling interrelationships of percentage of body moving during strike regressed against mass. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and slope differences from isometry (0.333) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. * Regressions were significant after Bonferroni correction.

				Slope dif. than zero?		Slope dif. than isometry?	
Data partition	*N*	$b \pm$ s.e.m.	r^2	^{t}observed	significance	^{t}observed	significance
Multiple strikes per species							
Multiple strikes per individual	66	-0.017 ± 0.058	0.001	-0.300	n. s.	6.034	$P < 0.001$*
Single value per individual (acceleration dataset)	17	0.131 ± 0.095	0.113	1.379	n. s.	2.126	n. s.
Single value per individual (velocity dataset)	17	0.130 ± 0.132	0.061	0.989	n. s.	1.538	n. s.
Non-calibrated species values							
Single best value (acceleration dataset)	6	0.215 ± 0.235	0.173	0.915	n. s.	0.502	n. s.
Single best value (velocity dataset)	6	0.346 ± 0.227	0.367	1.523	n. s.	0.057	n. s.
Mean value	6	0.023 ± 0.115	0.010	0.200	n. s.	2.696	n. s.
Independent contrasts							
Single best value (acceleration dataset)	5	0.221 ± 0.188	0.256	1.174	n. s..	0.596	n. s.
Single best value (velocity dataset)	5	0.309 ± 0.199	0.376	1.553	n. s.	0.121	n. s.
Mean value	5	0.261 ± 0.185	0.332	1.411	n. s.	0.389	n. s.

Table 52. Scaling interrelationships of percentage of body moving during strike regressed against snout-vent length. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and slope differences from isometry (1.0) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. * Regressions were significant after Bonferroni correction.

				Slope dif. than zero?		Slope dif. than isometry?	
Data partition	*N*	$b \pm$ s.e.m.	r^2	$t$observed	significance	$t$observed	significance
Multiple strikes per species							
Multiple strikes per individual	66	-0.087 ± 0.118	0.008	-0.740	n. s.	9.212	$P < 0.001$*
Single value per individual (acceleration dataset)	17	0.121 ± 0.203	0.023	0.594	n. s.	4.330	$P < 0.001$*
Single value per individual (velocity dataset)	17	0.276 ± 0.276	0.063	1.001	n. s.	2.623	$P < 0.02$
Non-calibrated species values							
Single best value (acceleration dataset)	6	0.195 ± 0.626	0.024	0.312	n. s.	1.286	n. s.
Single best value (velocity dataset)	6	1.042 ± 0.431	0.593	2.415	n. s.	0.097	n. s.
Mean value	6	0.487 ± 0.395	0.276	1.234	n. s.	1.299	n. s.
Independent contrasts							
Single best value (acceleration dataset)	5	0.279 ± 0.489	0.075	0.570	n. s.	1.474	n. s.
Single best value (velocity dataset)	5	1.000 ± 0.396	0.614	2.523	n. s.	0.000	n. s.
Mean value	5	0.565 ± 0.423	0.308	1.334	n. s.	1.028	n. s.

Table 53. Scaling interrelationships of time to maximum gape regressed against body mass. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and slope differences from isometry (0.333) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. * Regressions were significant after Bonferroni correction.

				Slope dif. than zero?		Slope dif. than isometry?	
Data partition	*N*	$b \pm$ s.e.m.	r^2	^{t}observed	significance	^{t}observed	significance
Multiple strikes per species							
Multiple strikes per individual	73	0.235 ± 0.113	0.057	2.074	$P < 0.05$	0.867	n. s.
Single value per individual (acceleration dataset)	18	0.582 ± 0.168	0.428	3.458	$P < 0.005$*	1.482	n. s.
Single value per individual (velocity dataset)	17	0.424 ± 0.199	0.232	2.131	$P < 0.05$	0.457	n. s.
Non-calibrated species values							
Single best value (acceleration dataset)	6	0.810 ± 0.514	0.383	1.575	n. s.	0.928	n. s.
Single best value (velocity dataset)	6	0.205 ± 0.246	0.148	0.834	n. s.	0.520	n. s.
Mean value	6	0.334 ± 0.168	0.496	1.984	n. s.	0.006	n. s.
Independent contrasts							
Single best value (acceleration dataset)	5	0.879 ± 0.563	0.379	1.561	n. s.	0.970	n. s.
Single best value (velocity dataset)	5	0.269 ± 0.253	0.220	1.063	n. s.	0.253	n. s.
Mean value	5	0.333 ± 0.166	0.502	2.007	n. s.	0.000	n. s.

Table 54. Scaling interrelationships of time to maximum gape regressed against snout-vent length. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and slope differences from isometry (1.0) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. * Regressions were significant after Bonferroni correction.

				Slope dif. than zero?		Slope dif. than isometry?	
Data partition	*N*	$b \pm$ s.e.m.	r^2	$t$observed	significance	$t$observed	significance
Multiple strikes per species							
Multiple strikes per individual	73	0.570 ± 0.228	0.081	2.499	$P < 0.02$	1.886	n. s.
Single value per individual (acceleration dataset)	18	1.225 ± 0.328	0.466	3.736	$P < 0.005$*	0.686	n. s.
Single value per individual (velocity dataset)	18	1.205 ± 0.352	0.439	3.424	$P < 0.005$*	0.582	n. s.
Non-calibrated species values							
Single best value (acceleration dataset)	6	2.117 ± 1.201	0.437	1.762	n. s.	0.93	n. s.
Single best value (velocity dataset)	6	0.689 ± 0.528	0.229	1.307	n. s.	0.589	n. s.
Mean value	6	0.686 ± 0.371	0.460	1.847	n. s.	0.846	n. s.
Independent contrasts							
Single best value (acceleration dataset)	5	2.337 ± 1.160	0.512	12.049	n. s.	1.187	n. s.
Single best value (velocity dataset)	5	1.000 ± 0.526	0.475	1.902	n. s.	0.000	n. s.
Mean value	5	0.671 ± 0.409	0.402	1.641	n. s.	0.804	n. s.

Table 55. Scaling interrelationships of time interval between maximum gape and initial prey contact regressed against body mass. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and slope differences from isometry (0.333) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. No regressions were significant after Bonferroni correction.

				Slope dif. than zero?		Slope dif. than isometry?	
Data partition	*N*	$b \pm$ s.e.m.	r^2	$t$observed	significance	$t$observed	significance
Multiple strikes per species							
Multiple strikes per individual	73	0.068 ± 0.234	0.001	0.292	n. s.	1.132	n. s.
Single value per individual (acceleration dataset)	18	1.298 ± 0.370	0.468	3.508	$P < 0.005$*	2.608	$P < 0.05$
Single value per individual (velocity dataset)	18	0.155 ± 0.349	0.012	0.444	n. s.	0.510	n. s.
Non-calibrated species values							
Single best value (acceleration dataset)	6	1.549 ± 0.809	0.478	1.913	n. s.	1.503	n. s.
Single best value (velocity dataset)	6	0.601 ± 0.201	0.691	2.988	$P < 0.05$	1.333	n. s.
Mean value	6	0.085 ± 0.098	0.157	0.864	n. s.	2.531	n. s.
Independent contrasts							
Single best value (acceleration dataset)	5	1.512 ± 0.769	0.492	1.967	n. s.	1.533	n. s.
Single best value (velocity dataset)	5	0.512 ± 0.194	0.635	2.638	n. s.	0.923	n. s.
Mean value	5	0.072 ± 0.105	0.107	0.691	n. s.	2.486	n. s.

Table 56. Scaling interrelationships of time interval between maximum gape and initial prey contact regressed against snout-vent length. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and slope differences from isometry (1.0) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. No regressions were significant after Bonferroni correction.

				Slope dif. than zero?		Slope dif. than isometry?	
Data partition	*N*	$b \pm$ s.e.m.	r^2	^{t}observed	significance	^{t}observed	significance
Multiple strikes per species							
Multiple strikes per individual	73	-0.067 ± 0.475	0.001	-0.140	n. s.	2.246	$P < 0.05$
Single value per individual (acceleration dataset)	18	2.206 ± 0.882	0.309	2.500	$P < 0.05$	1.367	n. s.
Single value per individual (velocity dataset)	18	0.382 ± 0.701	0.018	0.544	n. s.	0.882	n. s.
Non-calibrated species values							
Single best value (acceleration dataset)	6	2.176 ± 2.514	0.158	0.865	n. s.	0.468	n. s.
Single best value (velocity dataset)	6	1.476 ± 0.432	0.745	3.416	$P < 0.05$	1.102	n. s.
Mean value	6	0.160 ± 0.213	0.124	0.754	n. s.	3.944	P < 0.02
Independent contrasts							
Single best value (acceleration dataset)	5	2.016 ± 2.297	0.162	0.878	n. s.	0.442	n. s.
Single best value (velocity dataset)	5	1.292 ± 0.494	0.631	2.615	n. s.	0.591	n. s.
Mean value	5	0.118 ± 0.241	0.056	0.487	n. s.	3.660	$P < 0.05$

Table 57. Scaling interrelationships of time of lower jaw contact regressed against body mass. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and slope differences from isometry (0.333) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. * Regressions were significant after Bonferroni correction.

				Slope dif. than zero?		Slope dif. than isometry?	
Data partition	*N*	$b \pm$ s.e.m.	r^2	^{t}observed	significance	^{t}observed	significance
Multiple strikes per species							
Multiple strikes per individual	75	0.218 ± 0.110	0.051	1.988	n. s.	1.045	n. s.
Single value per individual (acceleration dataset)	18	0.638 ± 0.149	0.535	4.287	$P < 0.001$*	2.047	n. s.
Single value per individual (velocity dataset)	18	0.413 ± 0.172	0.264	2.396	$P < 0.05$	0.465	n. s.
Non-calibrated species values							
Single best value (acceleration dataset)	6	0.805 ± 0.472	0.421	1.706	n. s.	1.000	n. s.
Single best value (velocity dataset)	6	0.304 ± 0.204	0.357	1.491	n. s.	0.142	n. s.
Mean value	6	0.241 ± 0.131	0.460	1.845	n. s.	1.840	n. s.
Independent contrasts							
Single best value (acceleration dataset)	5	0.888 ± 0.498	0.443	1.784	n. s.	1.114	n. s.
Single best value (velocity dataset)	5	0.335 ± 0.193	0.429	1.732	n. s.	0.010	n. s.
Mean value	5	0.030 ± 0.019	0.394	1.612	n. s.	15.950	$P < 0.001$*

Table 58. Scaling interrelationships of time of lower jaw contact regressed against snout-vent length. $b \pm$ standard error of the mean (s.e.m.) and r^2 calculated from ordinary least squares regression. Slope differences from zero were determined using ANOVA and slope differences from isometry (1.0) were determined using modified test statistic from Zar (1984) with $\alpha = 0.05$ for both comparisons. * Regressions were significant after Bonferroni correction.

				Slope dif. than zero?		Slope dif. than isometry?	
Data partition	*N*	$b \pm$ s.e.m.	r^2	^{t}observed	significance	^{t}observed	significance
Multiple strikes per species							
Multiple strikes per individual	75	0.518 ± 0.221	0.070	2.347	$P < 0.05$	2.181	$P < 0.05$
Single value per individual (acceleration dataset)	18	1.302 ± 0.297	0.546	4.386	$P < 0.001$*	1.017	n. s.
Single value per individual (velocity dataset)	18	1.091 ± 0.300	0.453	3.638	$P < 0.002$*	0.303	n. s.
Non-calibrated species values							
Single best value (acceleration dataset)	6	2.083 ± 1.103	0.471	1.888	n. s.	0.982	n. s.
Single best value (velocity dataset)	6	0.868 ± 0.416	0.521	2.087	n. s.	0.317	n. s.
Mean value	6	-0.005 ± 0.056	0.002	-0.090	n. s.	17.946	$P < 0.001$*
Independent contrasts							
Single best value (acceleration dataset)	5	2.377 ± 0.997	0.587	2.385	n. s.	1.381	n. s.
Single best value (velocity dataset)	5	1.097 ± 0.494	0.716	3.177	$P < 0.05$	0.281	n. s.
Mean value	5	0.047 ± 0.049	0.188	0.963	n. s.	19.45	$P < 0.001$*

Table 59. Scaling exponents for total length (= snout-vent length in this study) when regressed against head length in six species of rattlesnakes. Data extrapolated from Table 19 of Klauber (1938) where data for *C. lepidus* is from *C. l. lepidus*, *C. viridis* is from *C. v. viridis*, *S. catenatus* is from *S. c. tergeminus*, and *S. miliarius* is from *S. m. streckeri*. In each study, head length was measured from the rostral scale to the posterior end of mandible at the retroarticular process. Data for both sexes are pooled for Klauber (1938), but presented separately in this study. Differential preservation effects may explain differences between the data sets because freshly killed specimens were analyzed by Klauber (1938) whereas fluid-preserved specimens were analyzed in the present study. Both adult and juvenile specimens were examined in each morphological analysis.

	Klauber (1938)	this study	
	combined sexes	males	females
Crotalus atrox	0.662	0.803	0.751
Crotalus lepidus	0.724	0.640	0.657
Crotalus viridis	0.665	0.701	0.719
Crotalus willardi	0.697	0.673	0.661
Sistrurus catenatus	0.671	0.698	0.718
Sistrurus miliarius	0.710	0.605	0.660

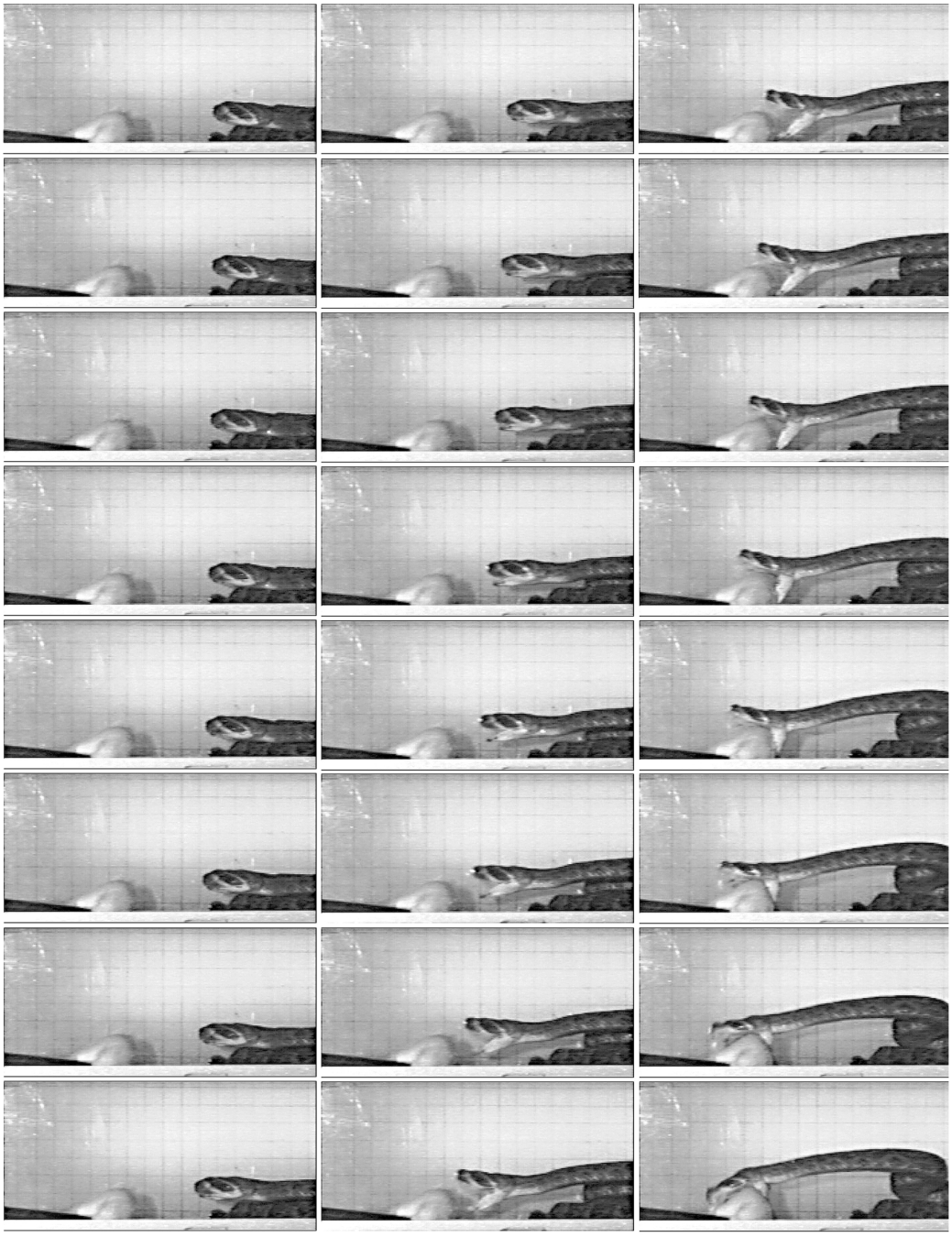


Figure 1. Sequences of video stills filmed at 1/1000 sec intervals depicting the predatory strike of *Crotalus atrox* toward a pre-killed rodent. Video stills are consecutive, though every other frame in the sequence has been removed (interval between video stills shown = 2 msec). Sequences progress from top to bottom, left to right.

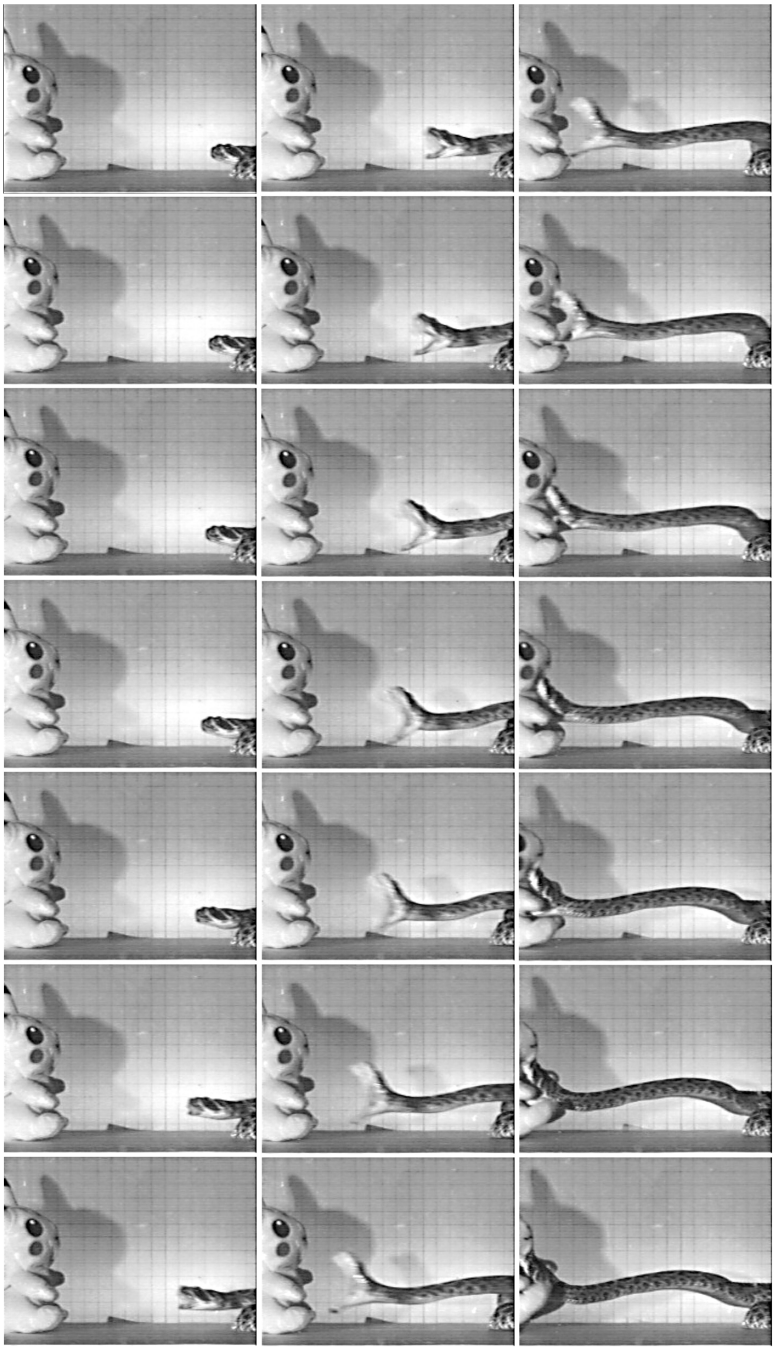


Figure 2. Sequences of consecutive video stills filmed at 1/500 sec intervals depicting the defensive strike of *Crotalus atrox* toward a kingsnake scented doll. Video stills are consecutive, though every other frame in the sequence has been removed (interval between video stills shown = 4 msec). Sequences progress from top to bottom, left to right.

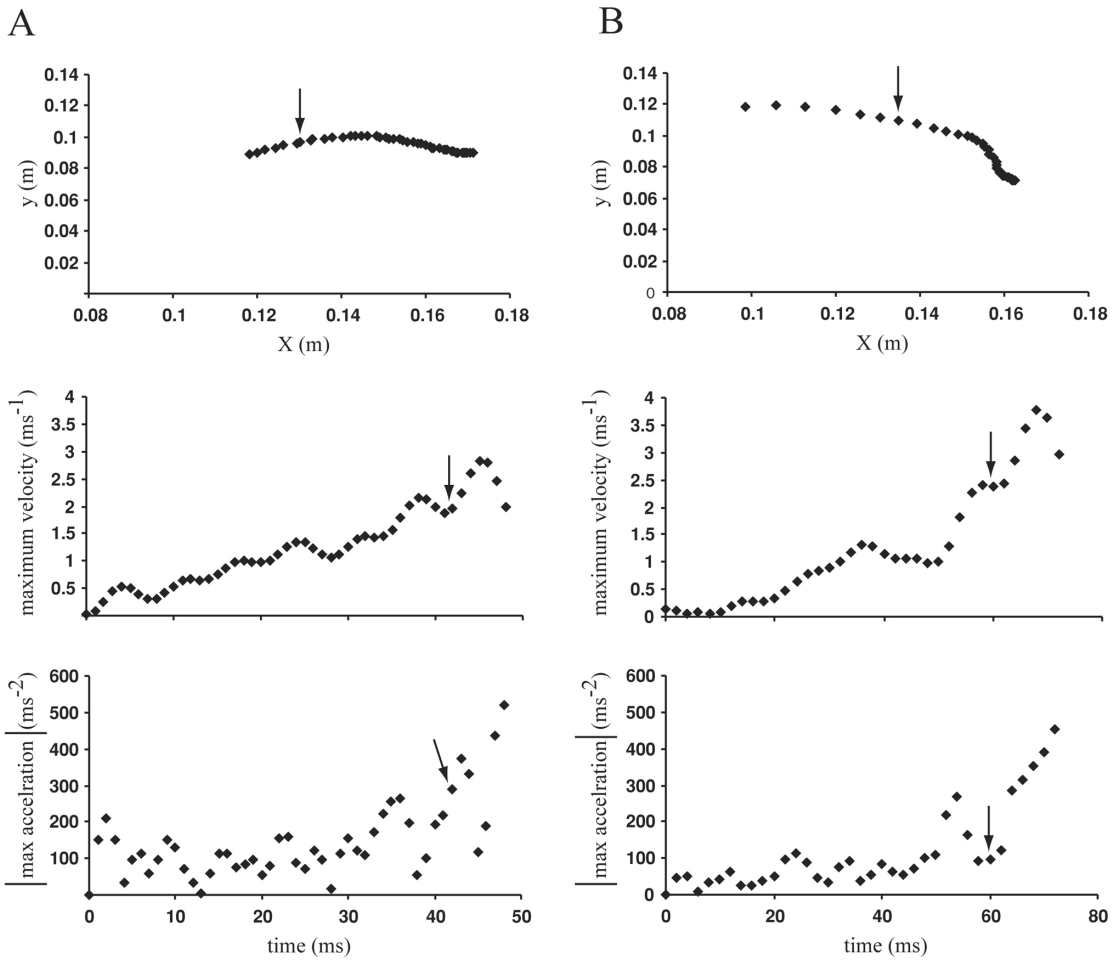


Figure 3. Movement, velocity, and acceleration of the snout of a single *Crotalus atrox* during extension and initial contact with a target during (A) a predatory strike, and (B) a defensive strike. In X-Y plots, movement is from right to left. Arrows in all graphs indicate point of initial jaw contact with the target, last data point marks point of secondary jaw contact.

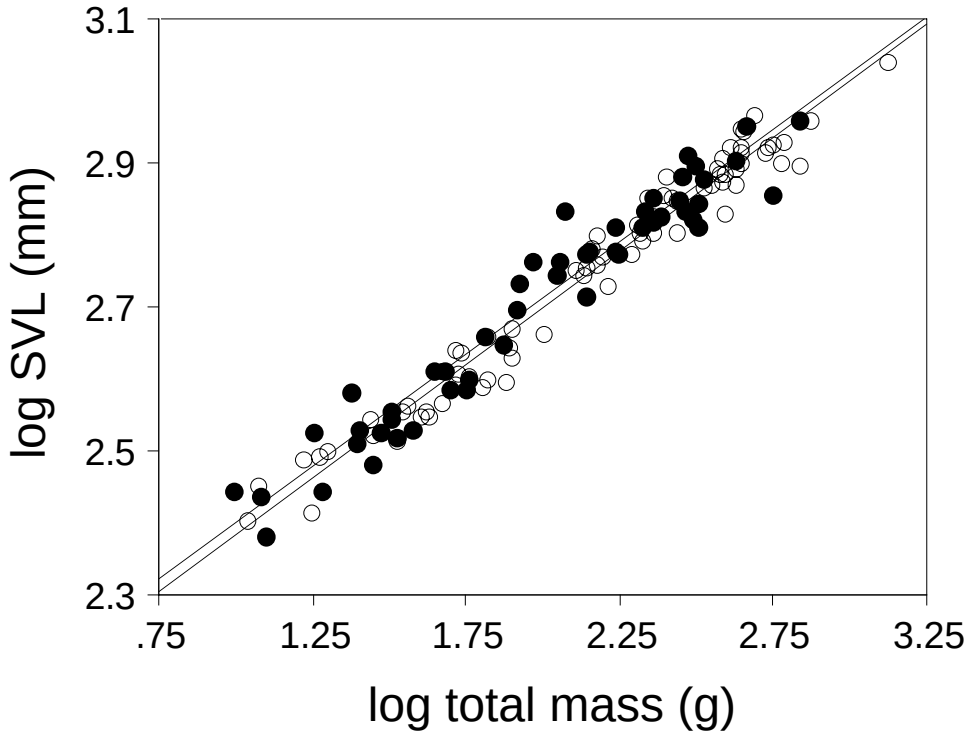


Figure 4. Log - log least square regression of snout-vent length (SVL) vs. total mass in preserved specimens of *Crotalus atrox*. Males are open circles (log SVL = 2.067 + 0.316(log total mass); $r^2 = 0.969$), females are closed circles (log SVL = 2.087 + 0.312(log total mass); $r^2 = 0.943$).

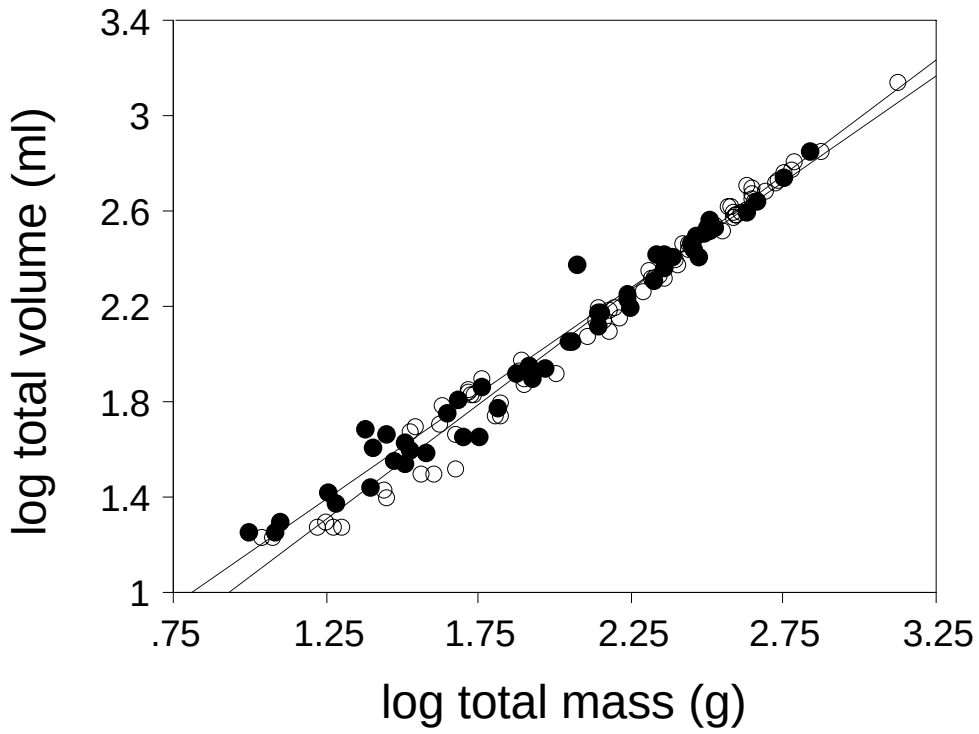


Figure 5. Log - log least square regression of total volume vs. total mass in preserved specimens of *Crotalus atrox*. Males are open circles (log total volume = 2.067 + 0.316(log total mass); $r^2 = 0.983$), females are closed circles (log total volume = 0.280 + 0.888(log total mass); $r^2 = 0.972$).

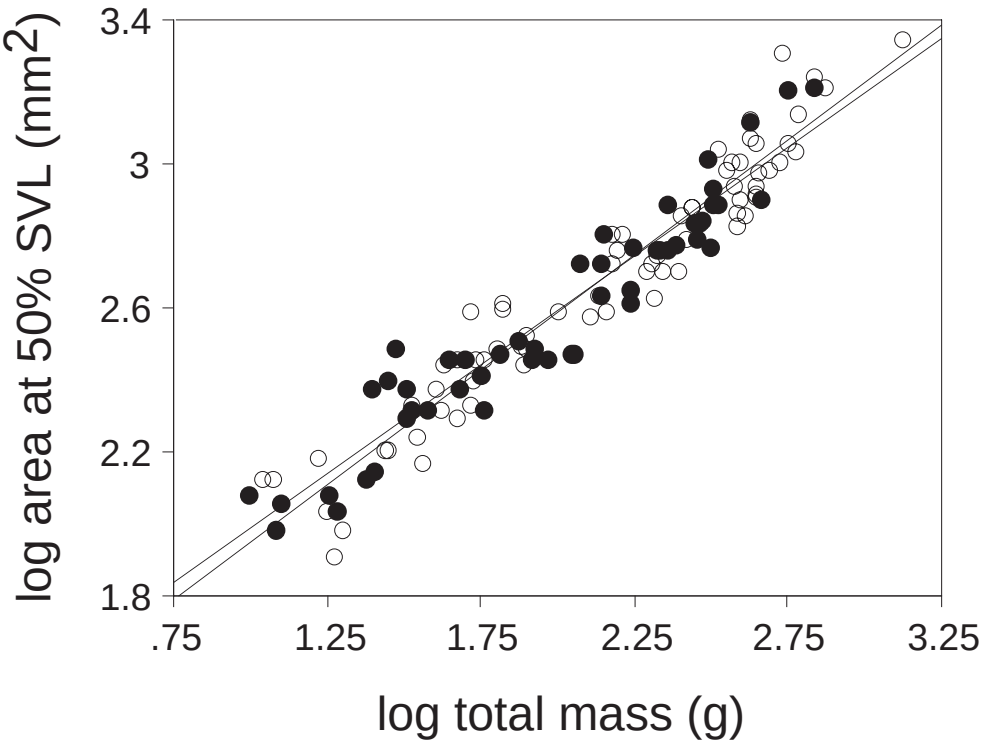


Figure 6. Log - log least square regression of estimated cross-sectional area at 50% snout-vent length vs. total mass in preserved specimens of *Crotalus atrox*. Males are open circles (log cross-sectional area at 50% SVL = 1.310 + 0.638(log total mass); r^2 = 0.927), females are closed circles (log cross-sectional area at 50% SVL = 1.383 + 0.604(log total mass); r^2 = 0.913).

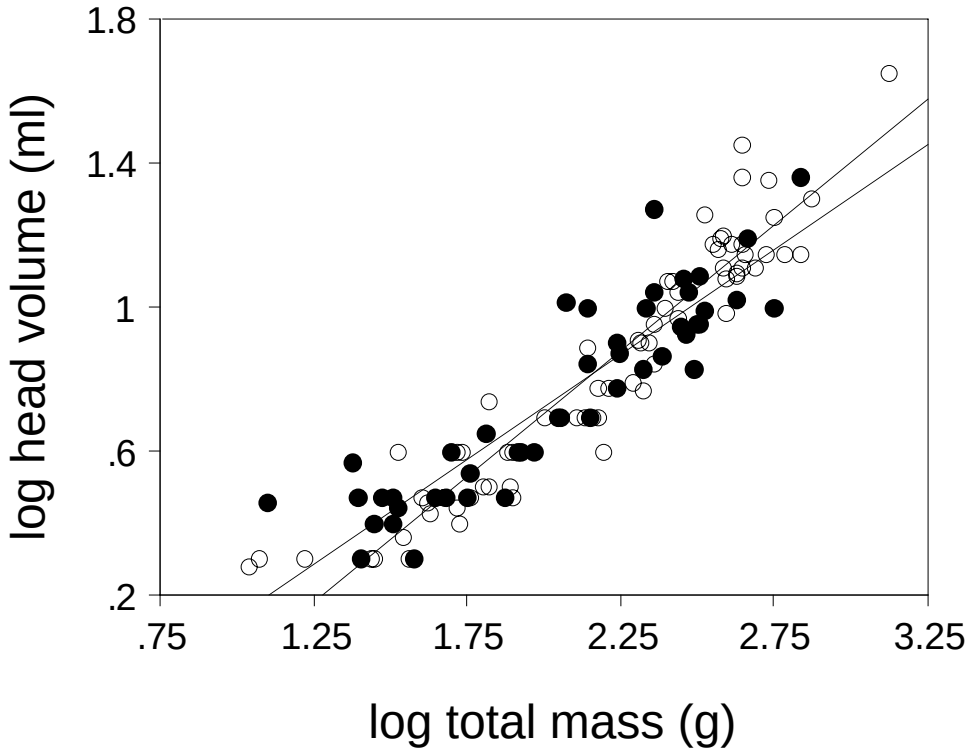


Figure 7. Log - log least square regression of head volume vs. total mass in preserved specimens of *Crotalus atrox*. Males are open circles (log head volume = -0.695 + 0.699(log total mass); $r^2 = 0.908$), females are closed circles (log head volume = -0.450 + 0.586(log total mass); $r^2 = 0.857$).

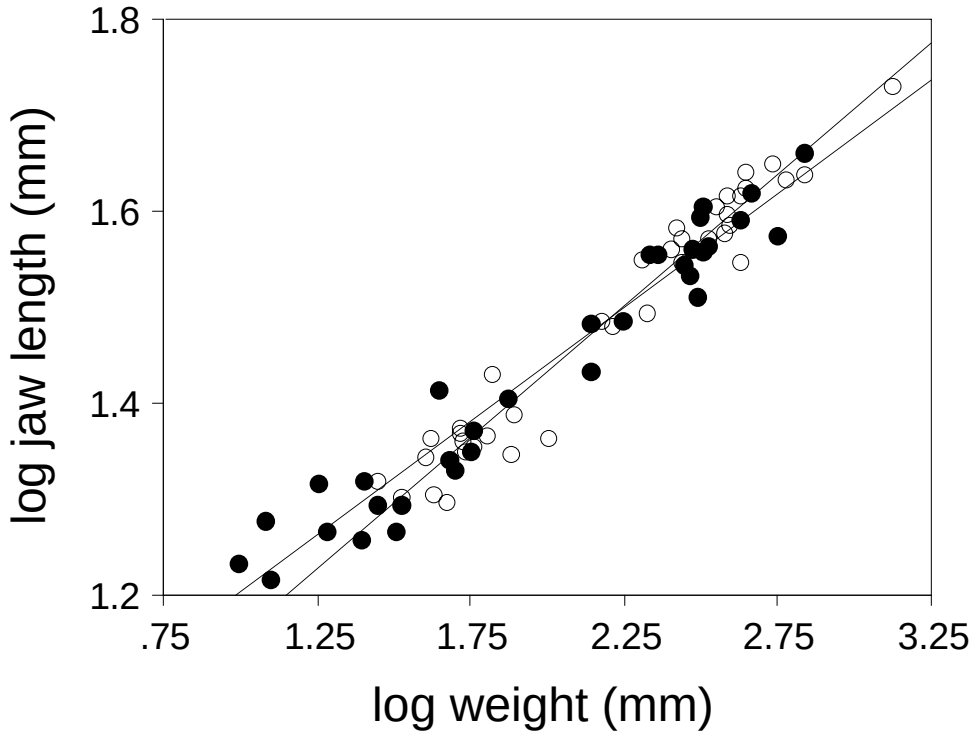


Figure 8. Log - log least square regression of jaw length vs. total mass in preserved specimens of *Crotalus atrox*. Males are open circles (log jaw length = 0.887 + 0.273(log total mass); $r^2 = 0.953$), females are closed circles (log jaw length = 0.968 + 0.236(log total mass); $r^2 = 0.945$).

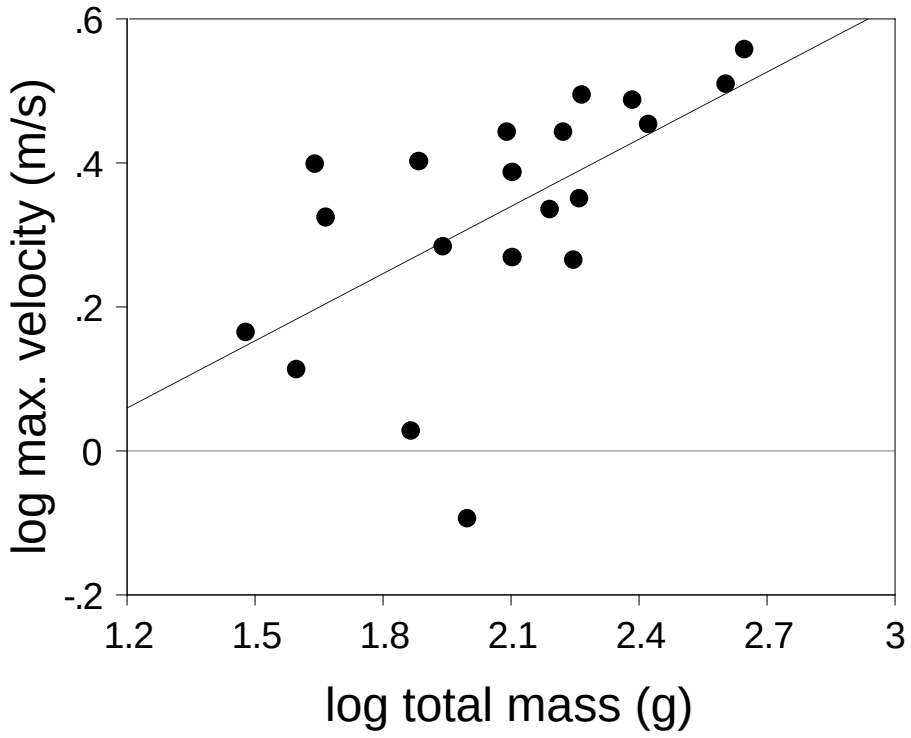


Figure 9. Log - log least square regression of maximum velocity vs. total mass for 20 specimens of *Crotalus atrox*. Single best value of maximum velocity used for each individual. Log maximum velocity = -0.313 + 0.310(log total mass); $r^2 = 0.354$.

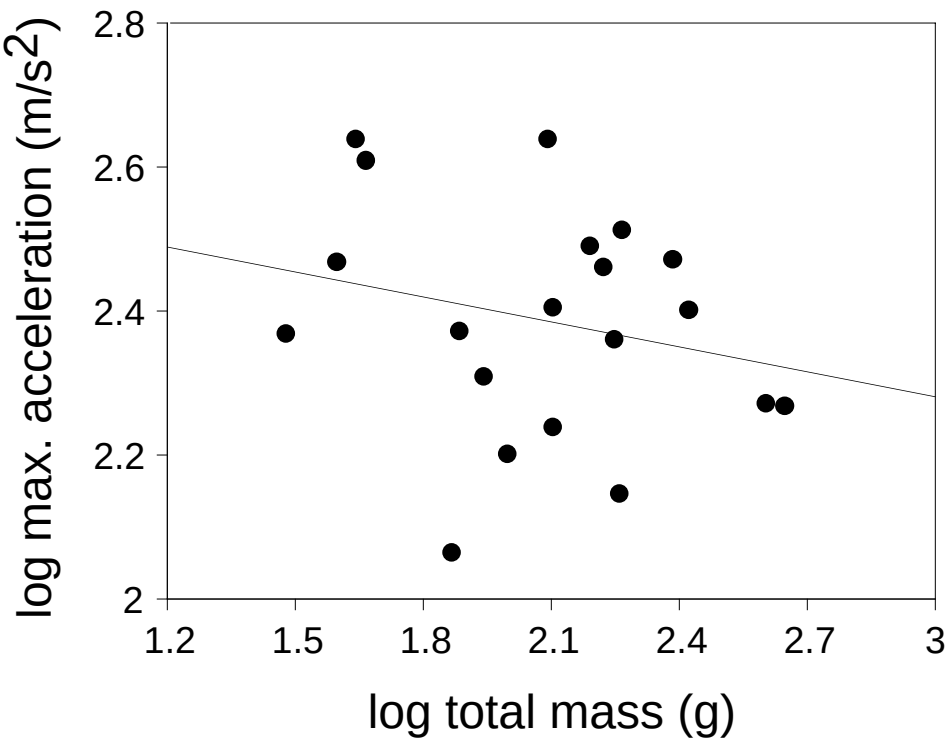


Figure 10. Log - log least square regression of maximum acceleration vs. total mass for 20 specimens of *Crotalus atrox*. Single best value of maximum acceleration used for each individual. Log maximum acceleration = 2.627 - 0.115(log total mass); $r^2 = 0.056$.

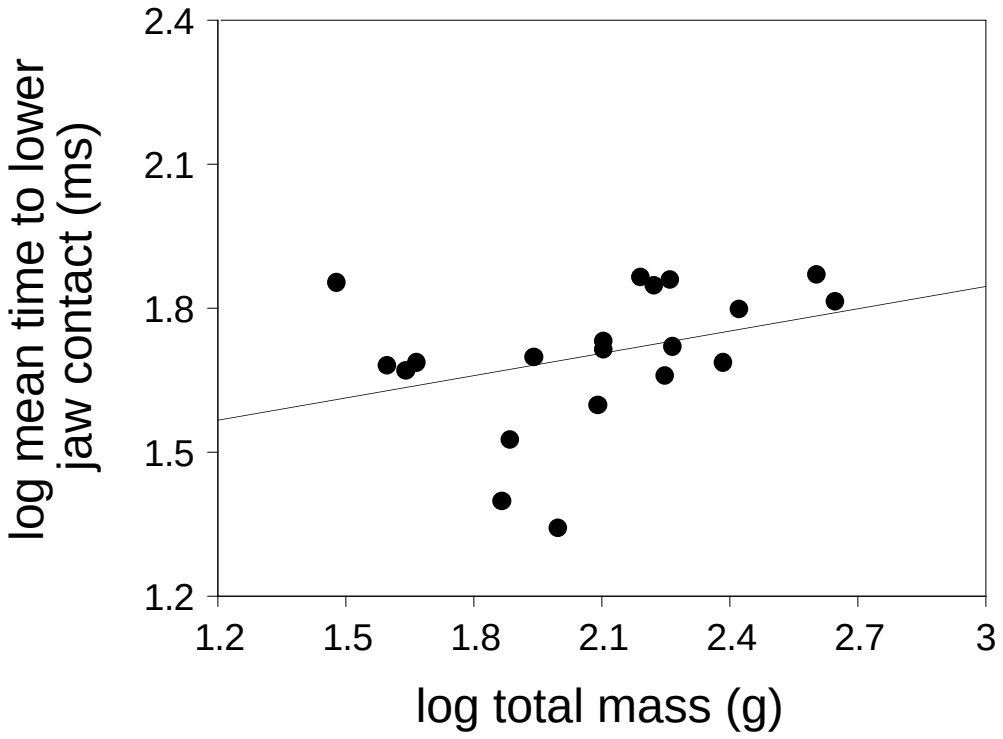


Figure 11. Log - log least square regression of mean time to lower jaw contact vs. total mass for 20 specimens of *Crotalus atrox*. Log mean time to lower jaw contact = 1.378 + 0.156(log total mass); $r^2 = 0.118$.

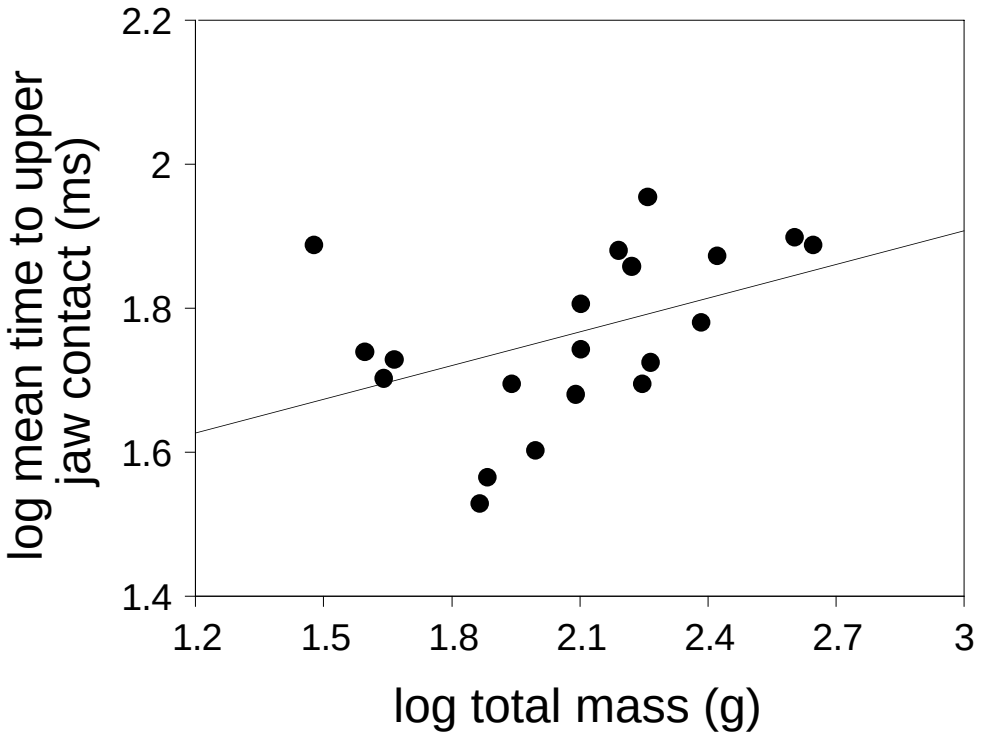


Figure 12. Log - log least square regression of mean time to upper jaw contact vs. total mass for 20 specimens of *Crotalus atrox*. Log mean time to upper jaw contact = 1.438 + 0.156(log total mass); $r^2 = 0.185$.

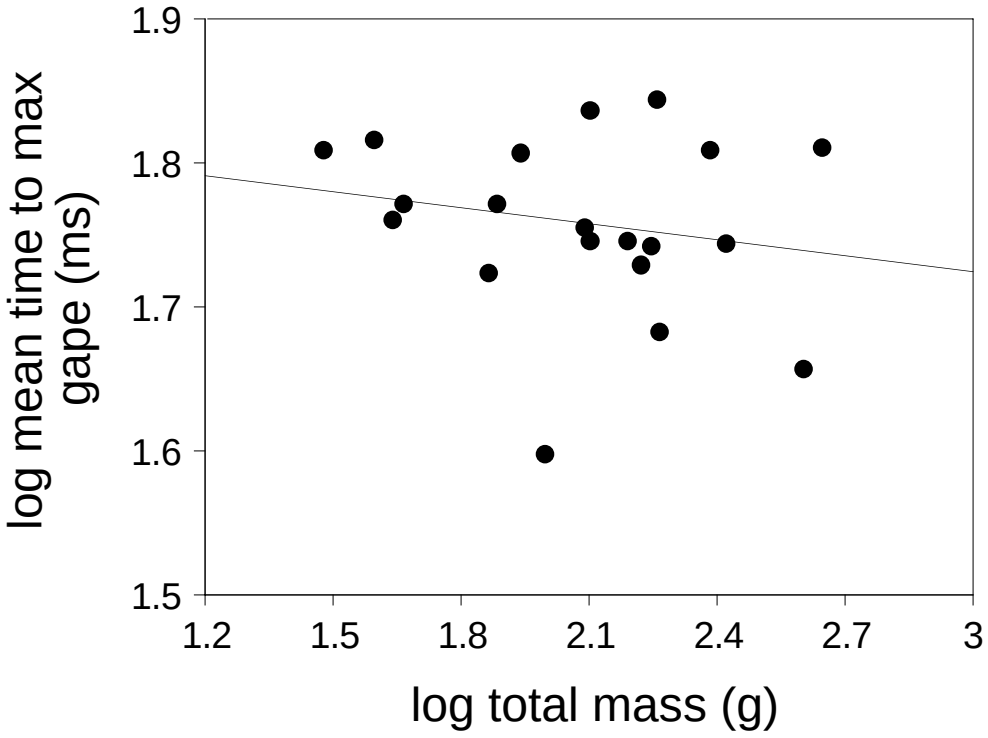


Figure 13. Log - log least square regression of mean time to maximum gape vs. total mass for 20 specimens of *Crotalus atrox*. Log mean time to maximum gape = 1.834 - 0.036(log total mass); $r^2 = 0.037$.

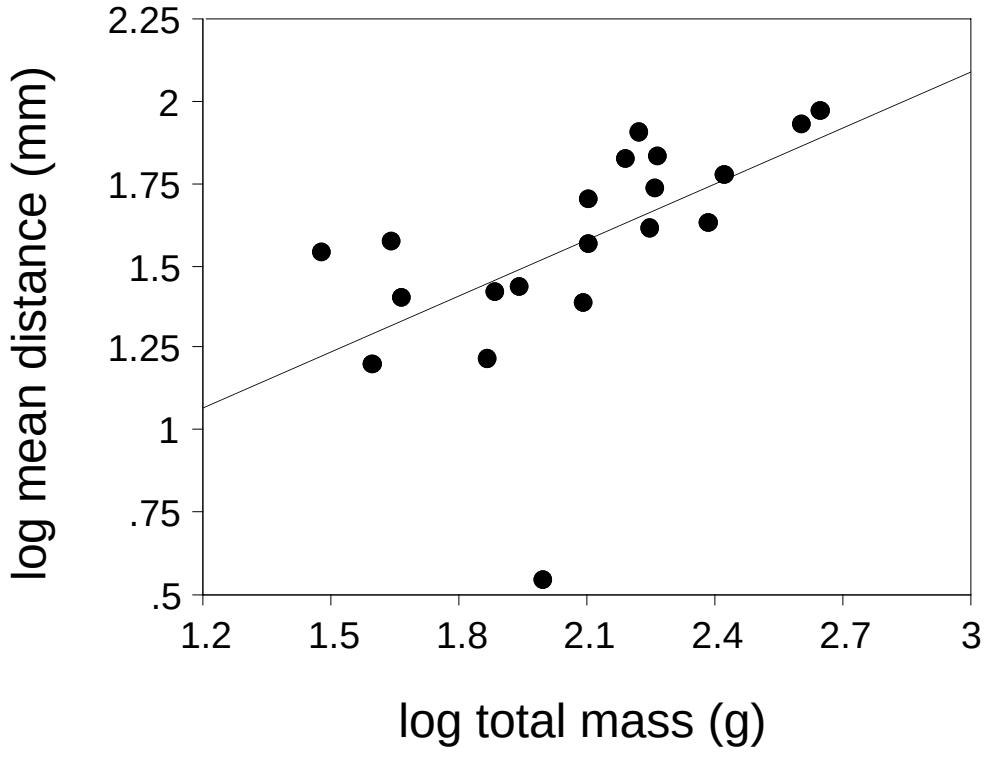


Figure 14. Log - log least square regression of mean strike distance vs. total mass for 20 specimens of *Crotalus atrox*. Log mean strike distance = 0.389 + 0.566(log total mass); $r^2 = 0.315$.

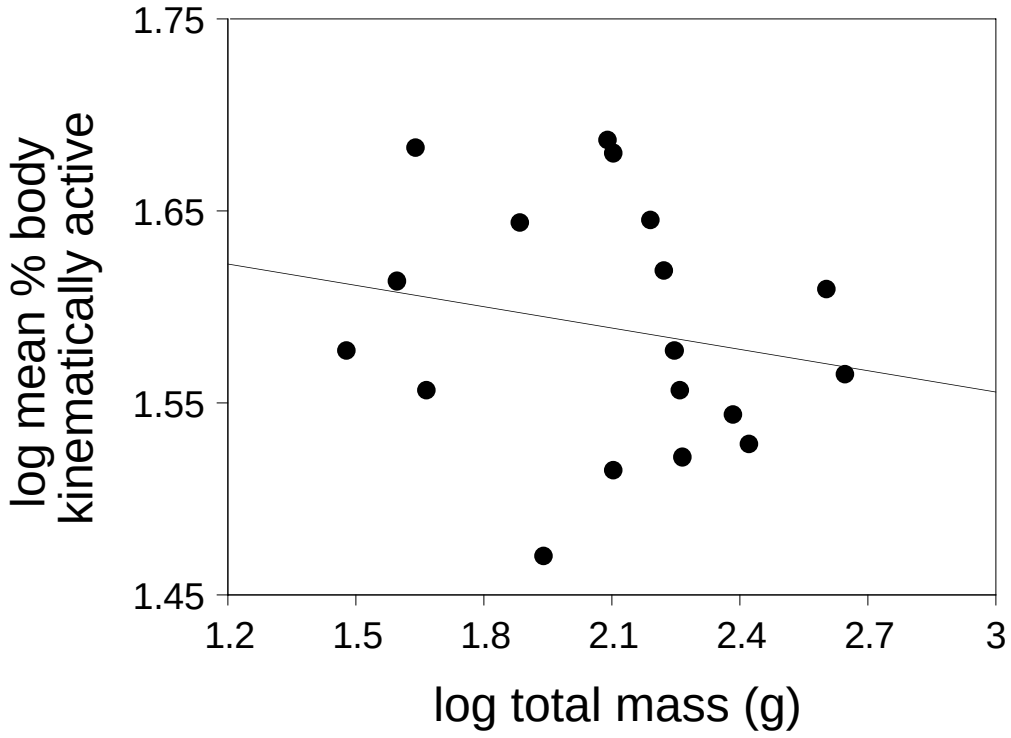


Figure 15. Log - log least square regression of mean portion of body kinematically active during the strike vs. total mass for 20 specimens of *Crotalus atrox*. Log mean portion of body kinematically active during strike = 1.667 - 0.370(log total mass); r^2 = 0.040.

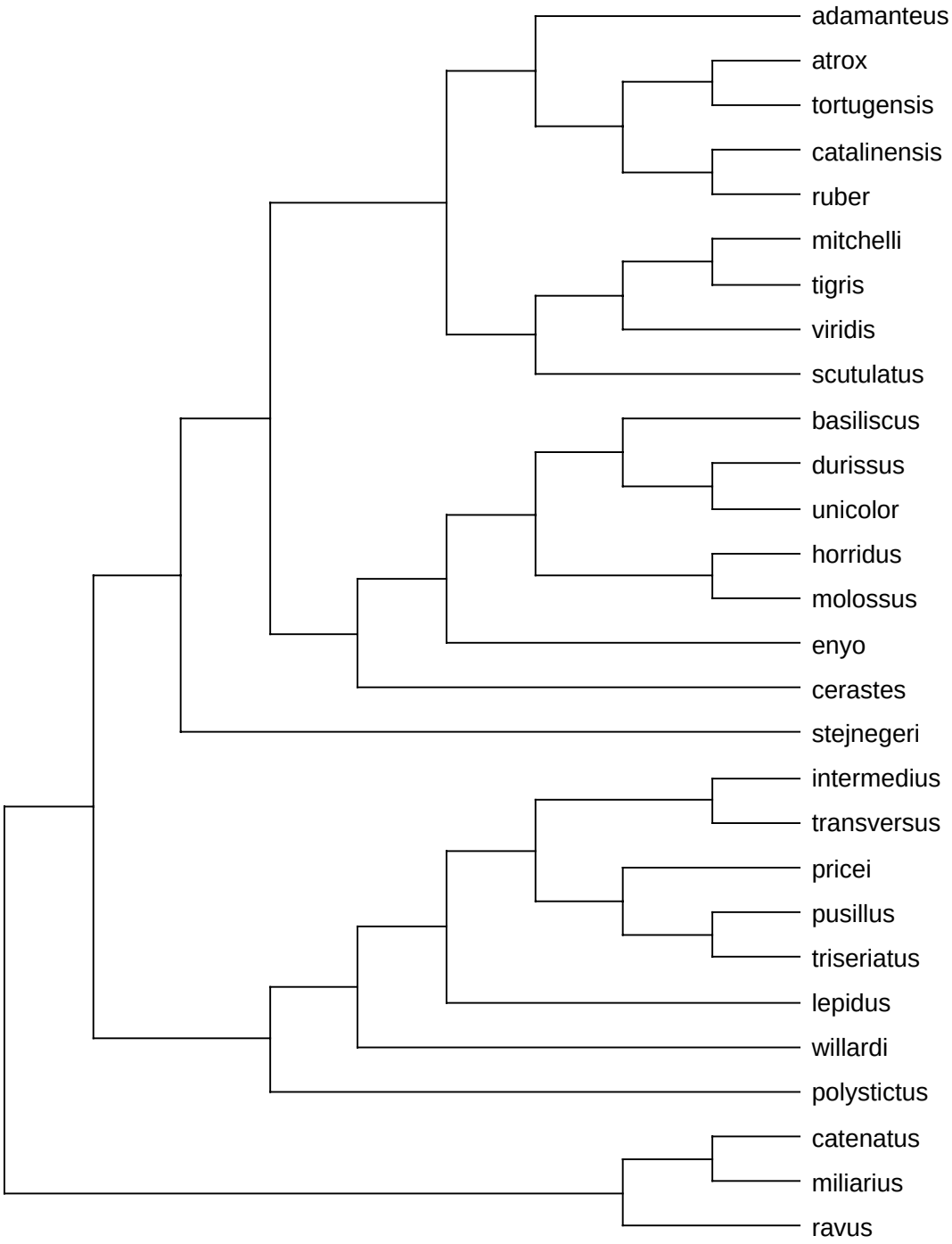


Figure 16. Estimate of rattlesnake relationships from Klauber (1956) used as constraint tree for Templeton test comparisons.

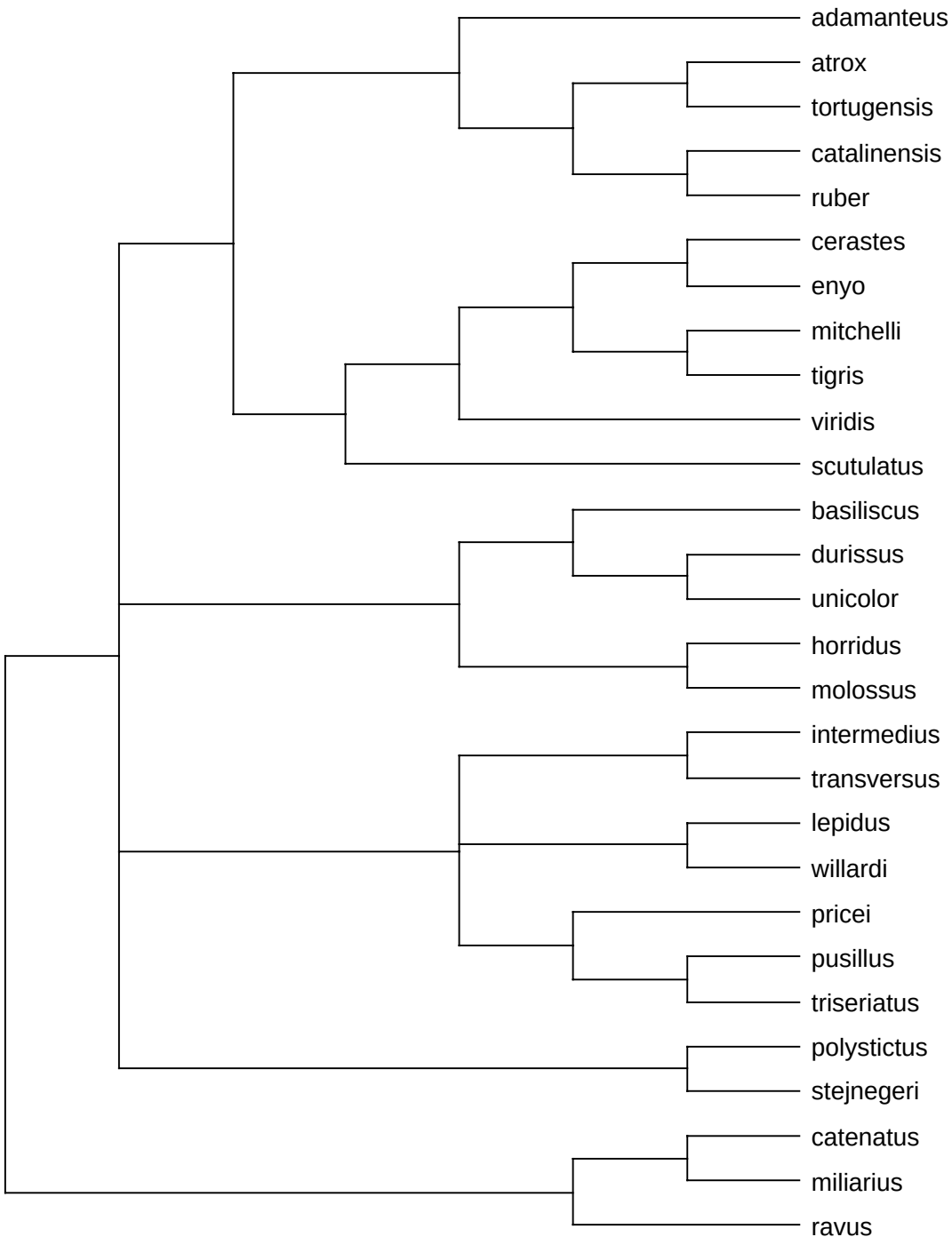


Figure 17. Estimate of rattlesnake relationships from Brattstrom (1964) used as constraint tree for Templeton test comparisons.

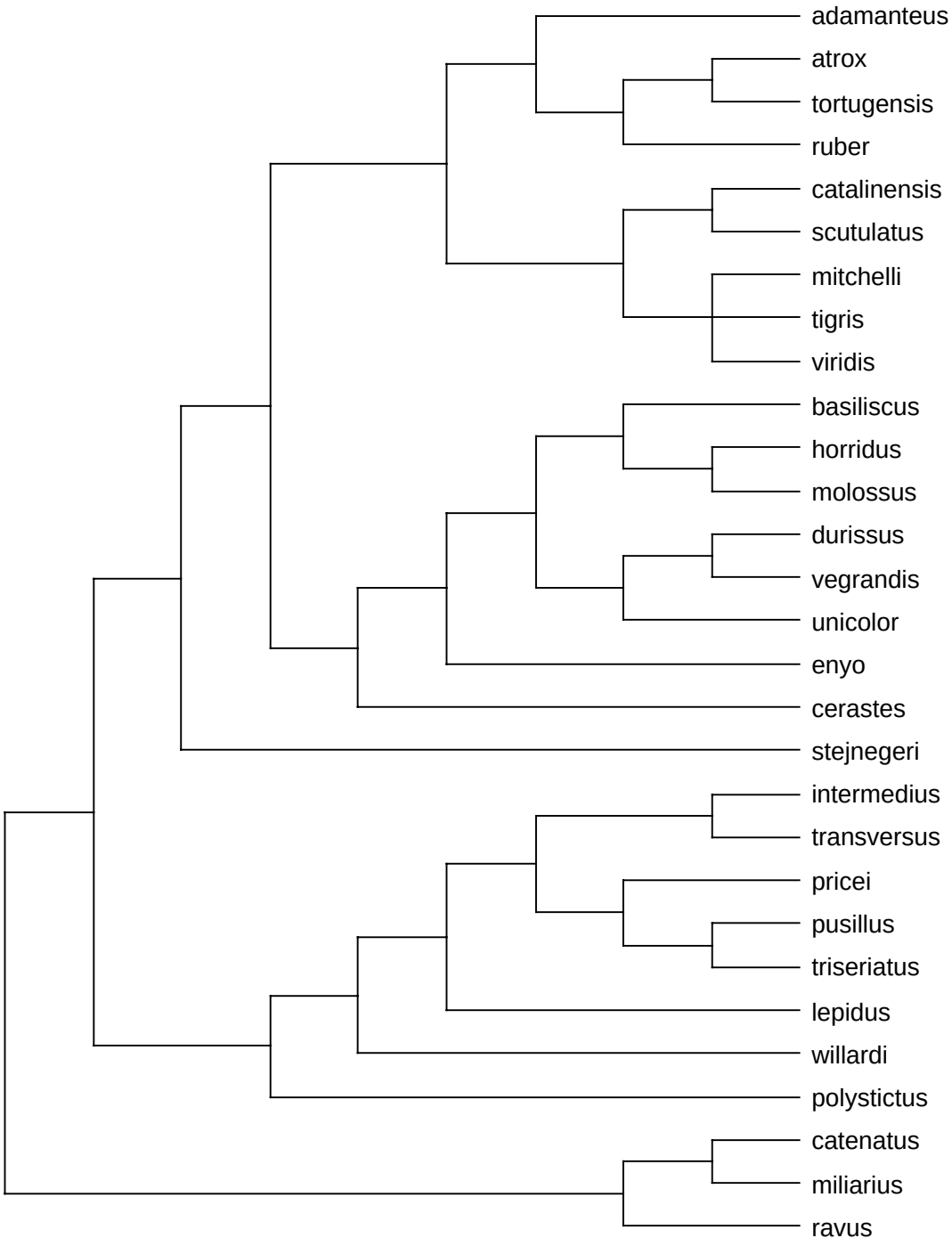


Figure 18. Estimate of rattlesnake relationships from Klauber (1972) used as constraint tree for Templeton test comparisons.

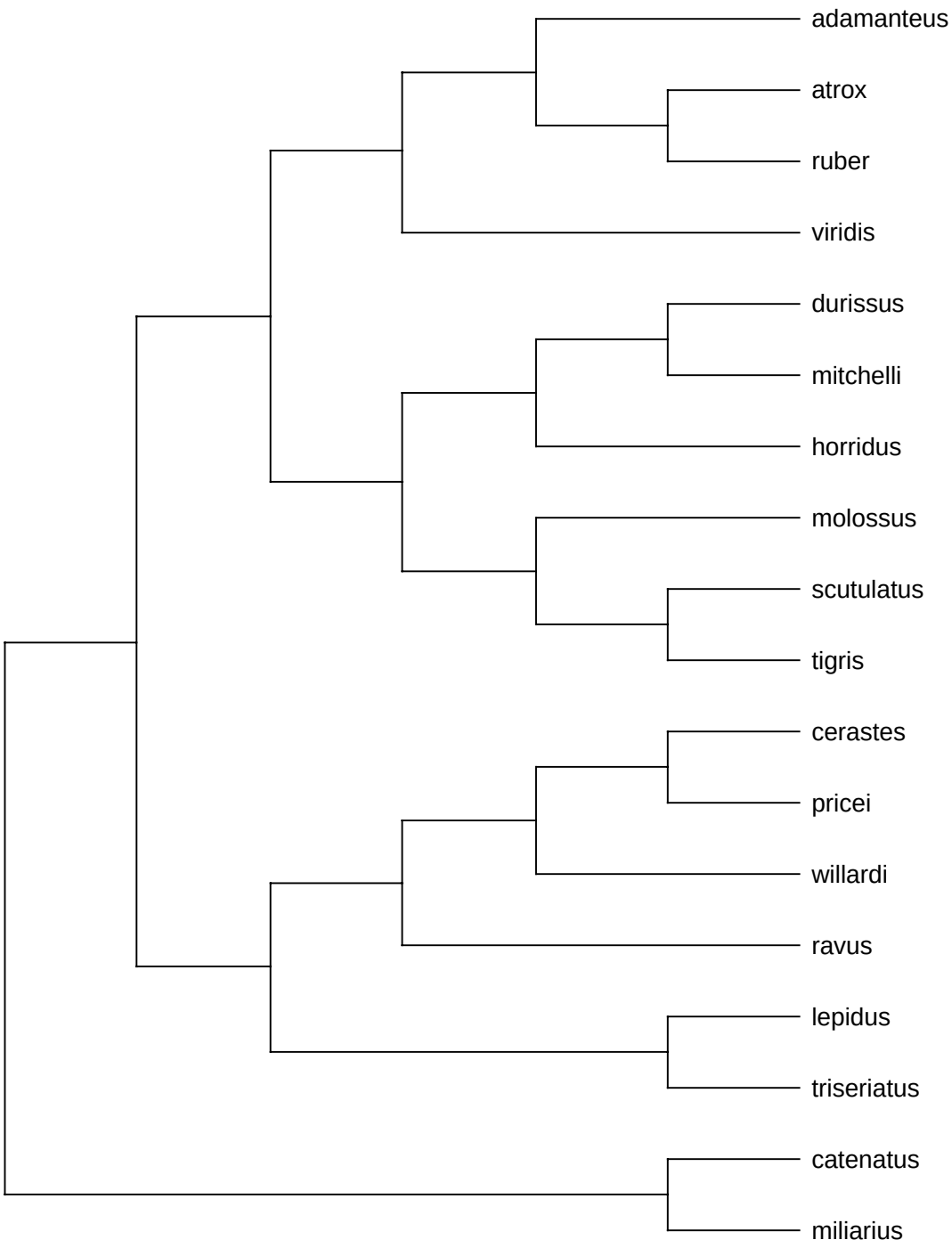


Figure 19. Estimate of rattlesnake relationships from Foote and MacMahon (1977) used as constraint tree for Templeton test comparisons.

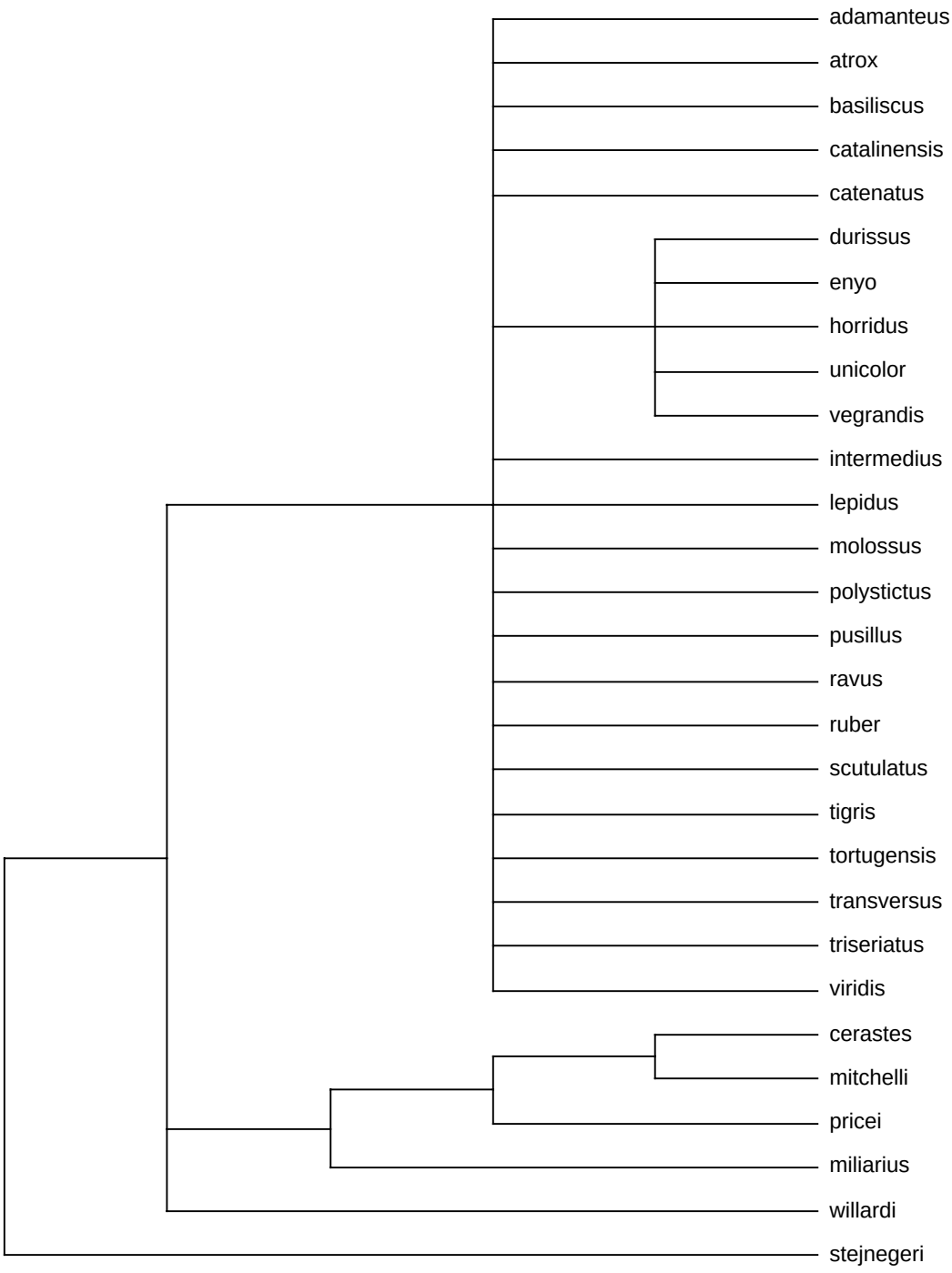


Figure 20. Estimate of rattlesnake relationships from Stille (1987) used as constraint tree for Templeton test comparisons.

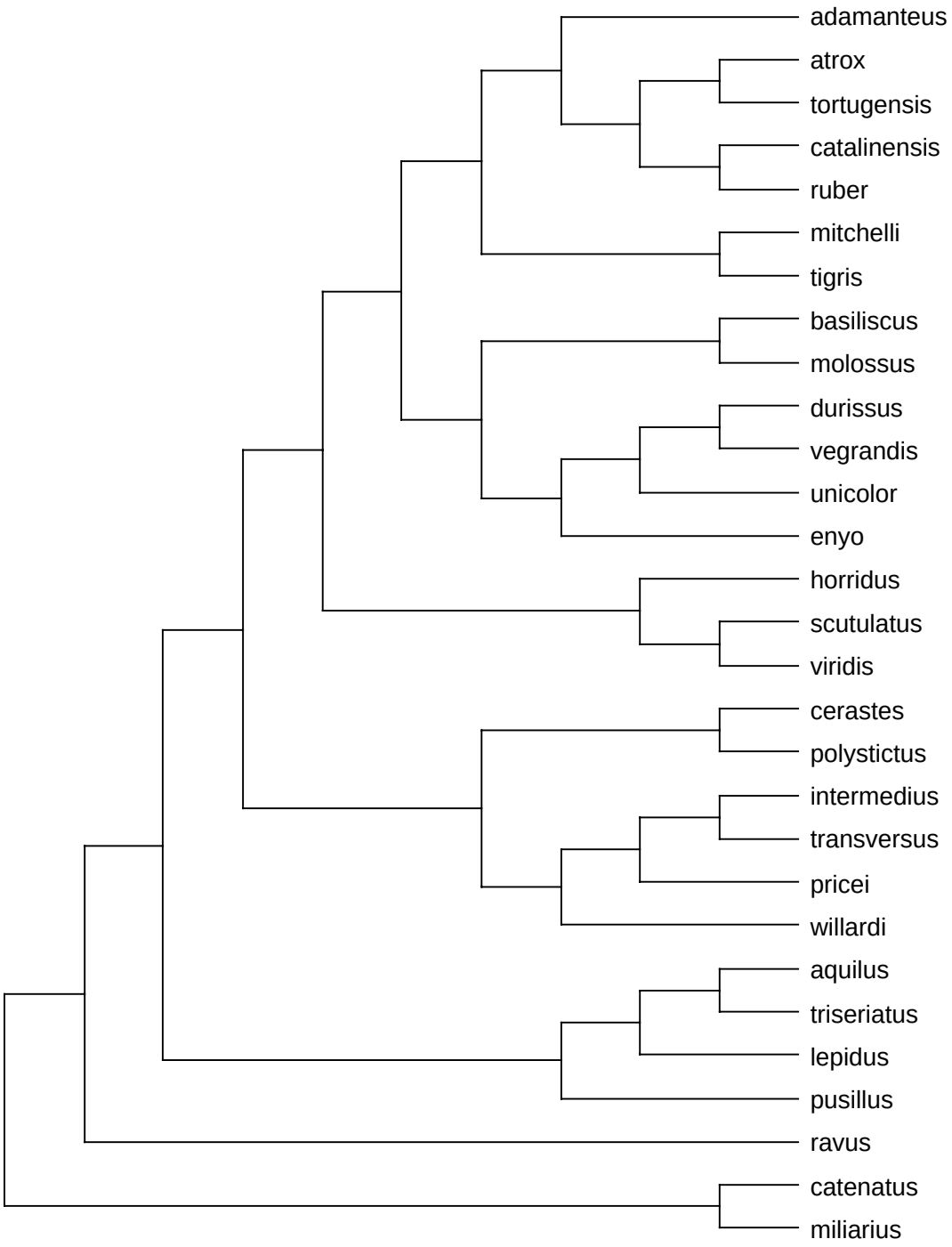


Figure 21. Estimate of rattlesnake relationships from Murphy et al. (2002) used as constraint tree for Templeton test comparisons.

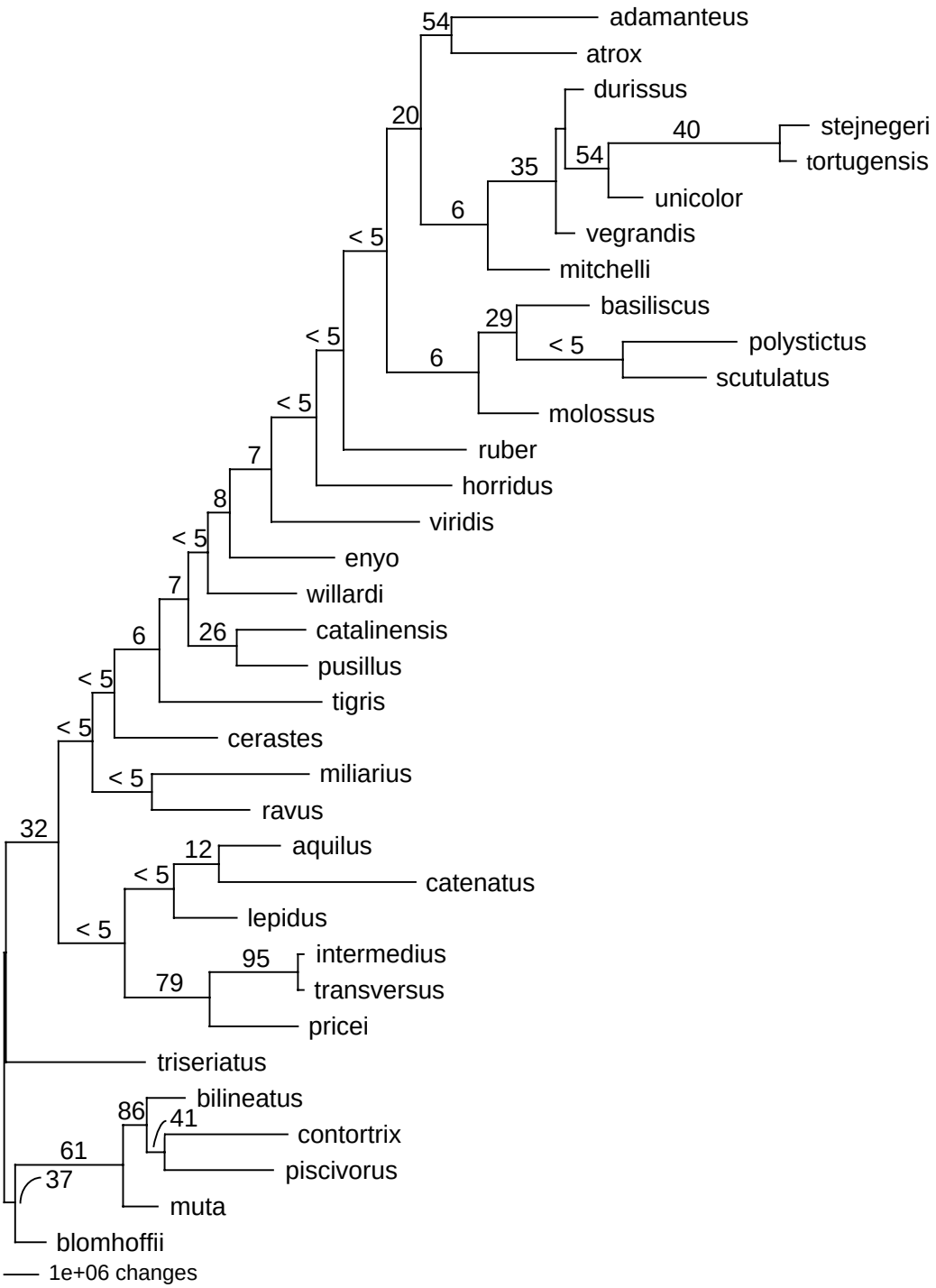


Figure 22. The single most-parsimonious tree found for the rattlesnakes using only the morphological (311 characters) data set. Numbers above nodes are bootstrap values for support of nodes.

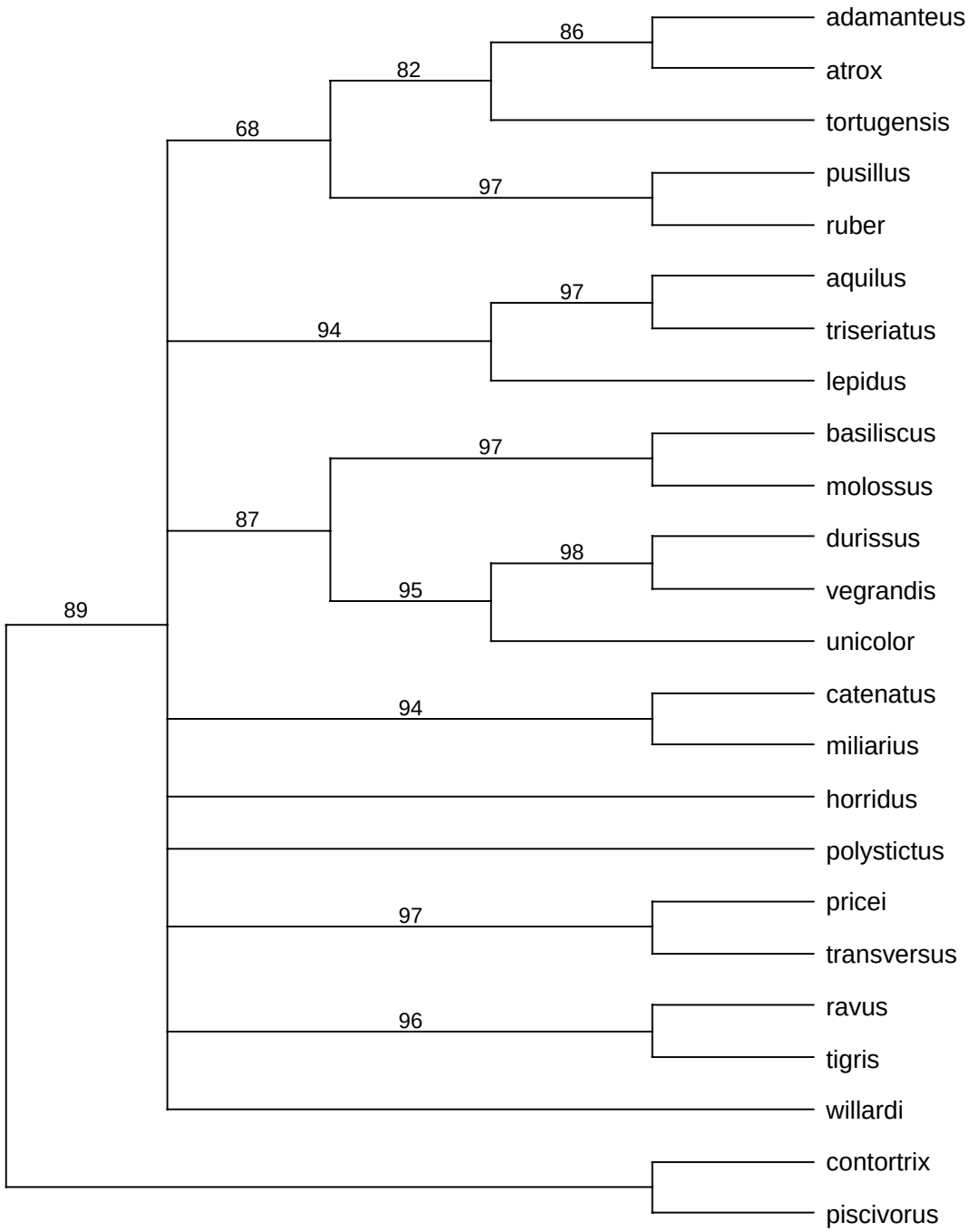


Figure 23. A majority-rule consensus tree for the 249 most-parsimonious trees found for the rattlesnakes using only the ND5 sequence (477 characters) data set. Eleven taxa for which no sequence data were available were excluded (*Crotalus catalinensis*, *C. cerastes*, *C. enyo*, *C. intermedius*, *C. mitchellii*, C. *scutulatus*, *C. stejnegeri*, *C. viridis*, *Agkistrodon bilineatus*, *Lachesis muta*, and *Gloydius blomhoffii*). Numbers above nodes are bootstrap values for support of nodes.

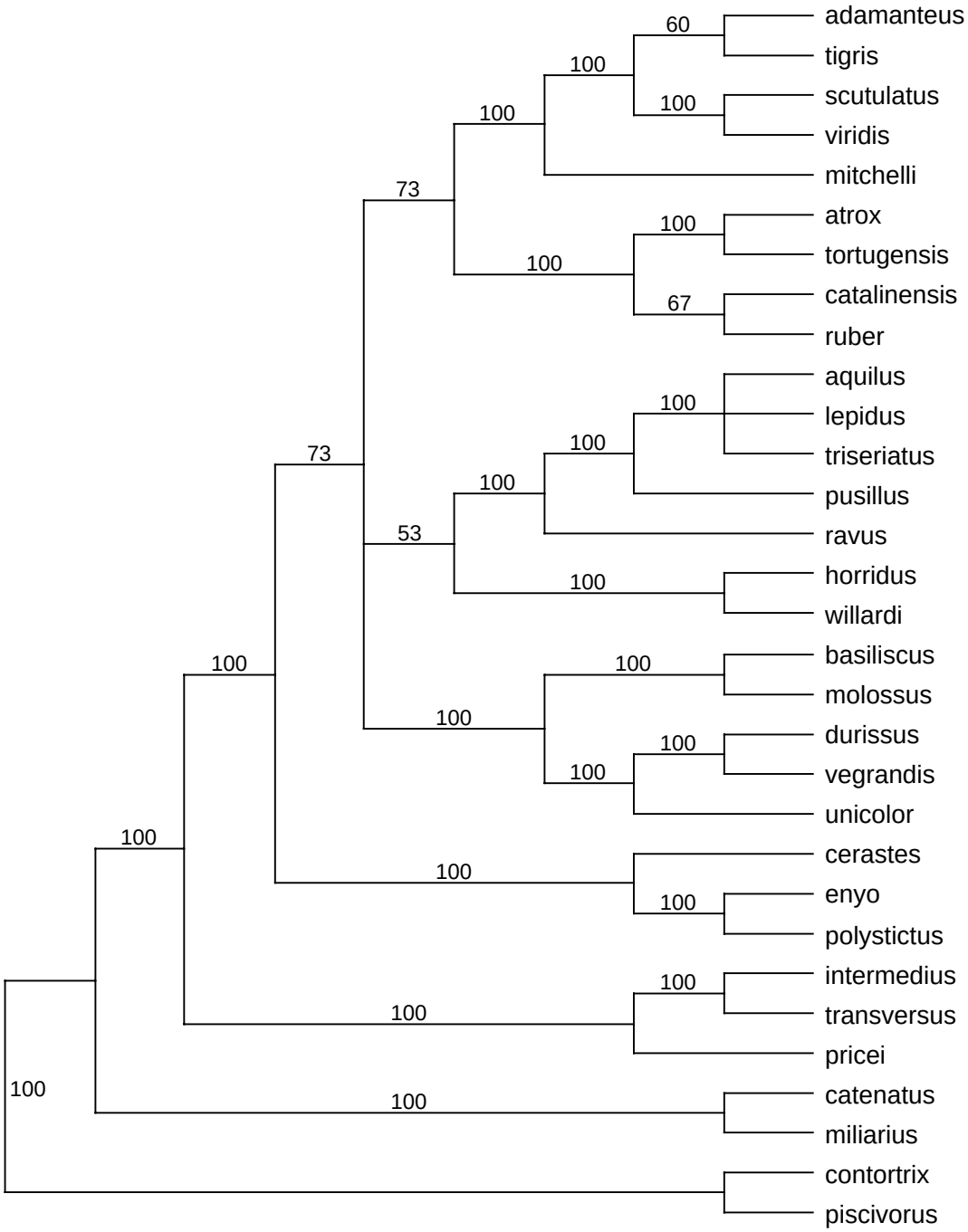


Figure 24. A majority-rule consensus tree for the 15 most-parsimonious trees found for the rattlesnakes using only the 12S/tRNA^{Val}/16S sequence (1905 characters with 96 ambiguously aligned sites included) data set. Four taxa for which no sequence data were available were excluded (*Crotalus stejnegeri*, *Agkistrodon bilineatus*, *Lachesis muta*, and *Gloydius blomhoffii*). Numbers above nodes are bootstrap values for support of nodes.

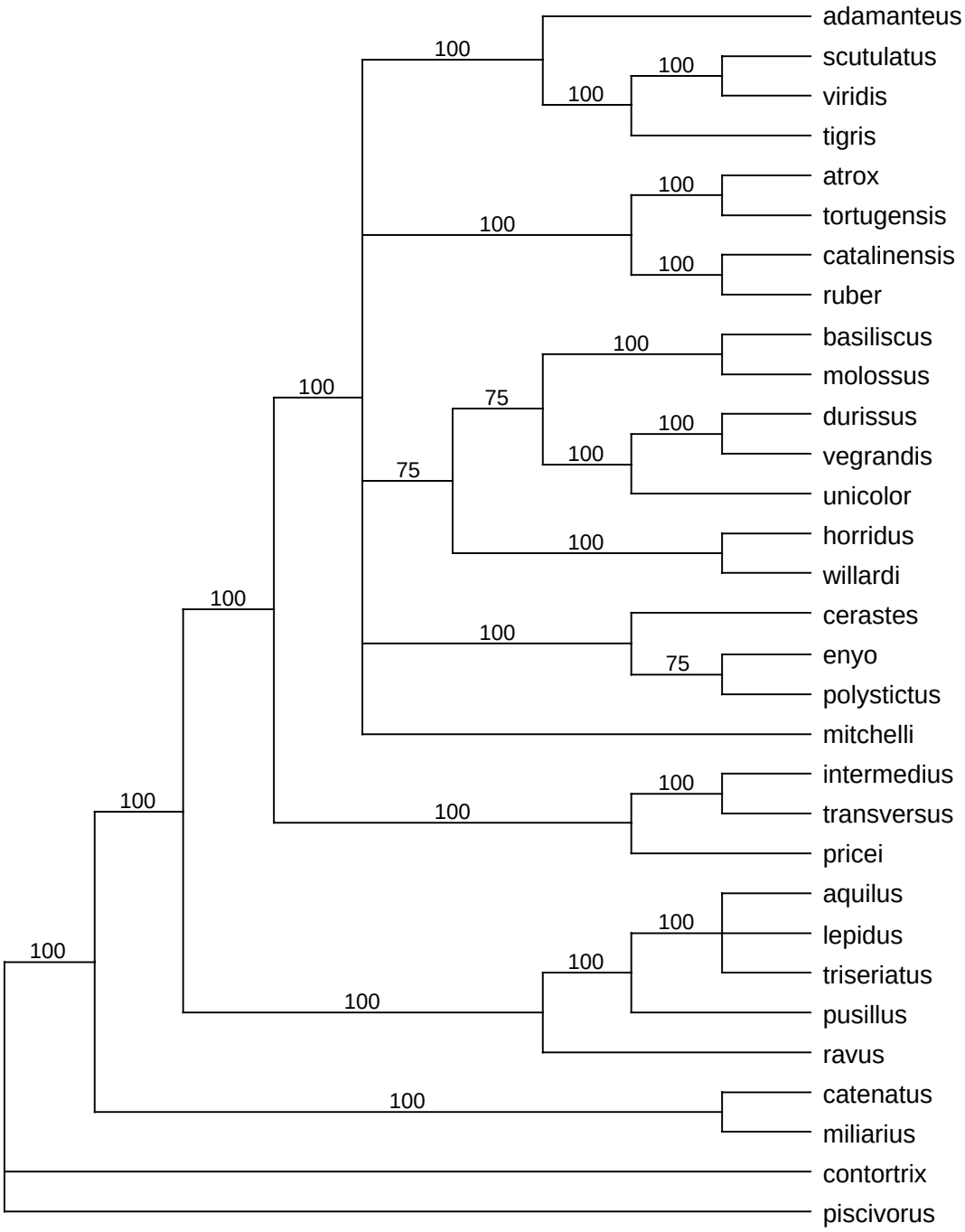


Figure 25. A majority-rule consensus tree for the 12 most-parsimonious trees found for the rattlesnakes using only the 12S/tRNA^{Val}/16S sequence (1809 characters with 96 ambiguously aligned sites excluded) data set. Four taxa for which no sequence data were available were excluded (*Crotalus stejnegeri*, *Agkistrodon bilineatus*, *Lachesis muta*, and *Gloydius blomhoffii*). Numbers above nodes are bootstrap values for support of nodes.

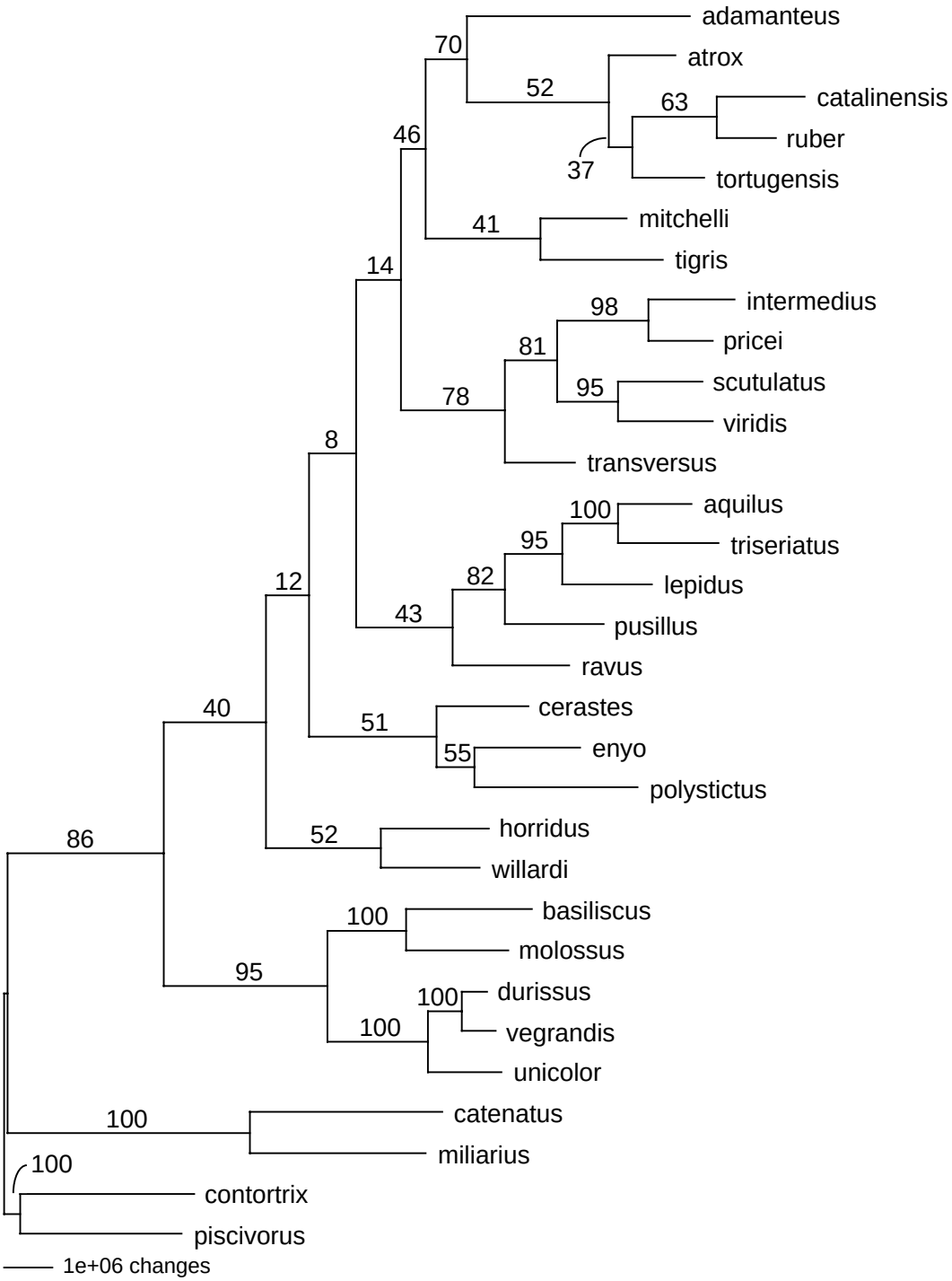


Figure 26. The single most-parsimonious tree found for the rattlesnakes using only the 12S/tRNA^{Val}/16S and ND5 sequence (2382 characters with 96 ambiguously aligned sites included) data sets. Four taxa for which no sequence data were available were excluded (*Crotalus stejnegeri*, *Agkistrodon bilineatus*, *Lachesis muta*, and *Gloydius blomhoffii*). Numbers above nodes are bootstrap values for support of nodes.

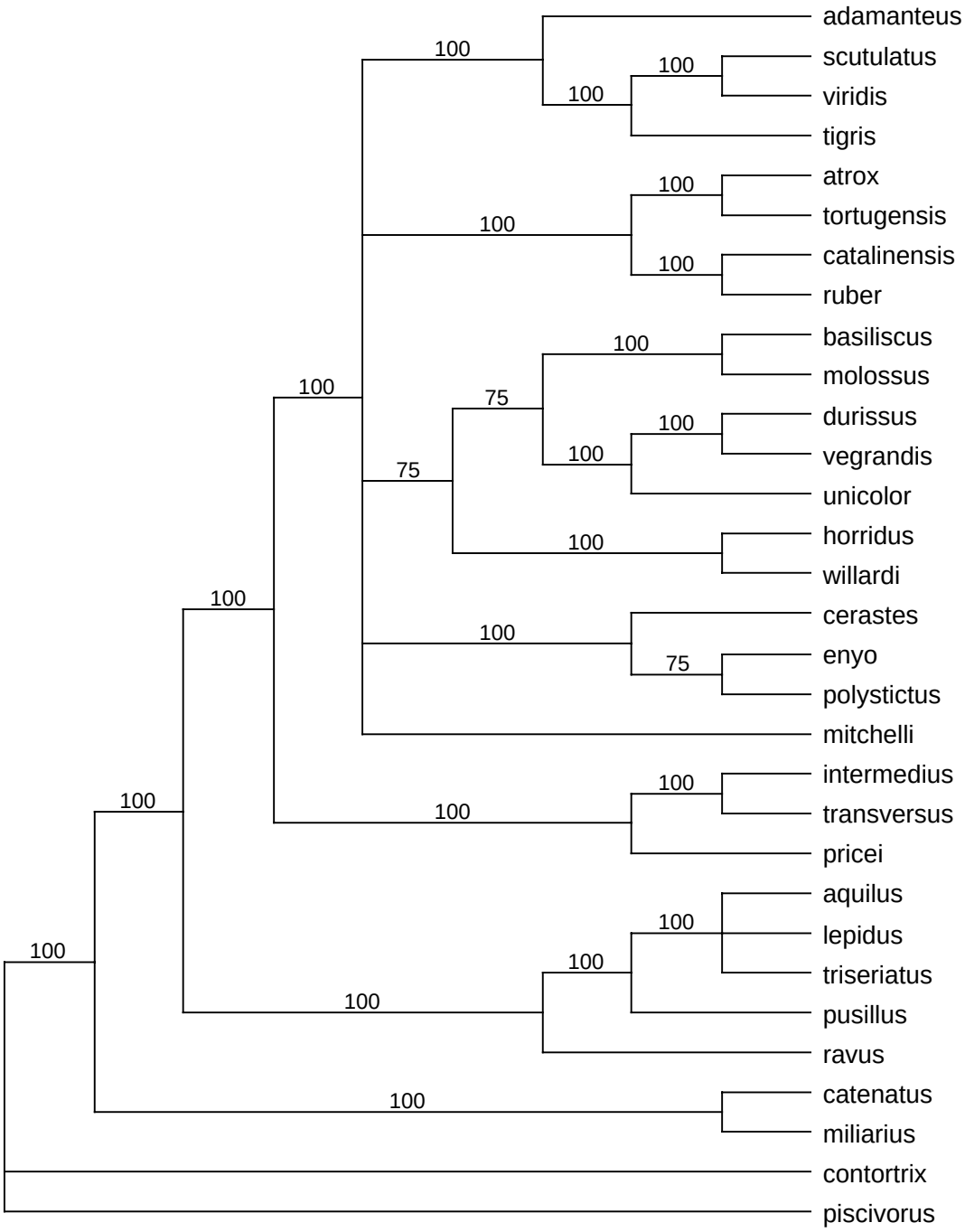


Figure 27. A majority-rule consensus tree for the 6 most-parsimonious trees found for the rattlesnakes using only the 12S/tRNA^{Val}/16S and ND5 sequence (2286 characters with 96 ambiguously aligned sites excluded) data sets. Four taxa for which no sequence data were available were excluded (*Crotalus stejnegeri*, *Agkistrodon bilineatus*, *Lachesis muta*, and *Gloydius blomhoffii*). Numbers above nodes are bootstrap values for support of nodes.

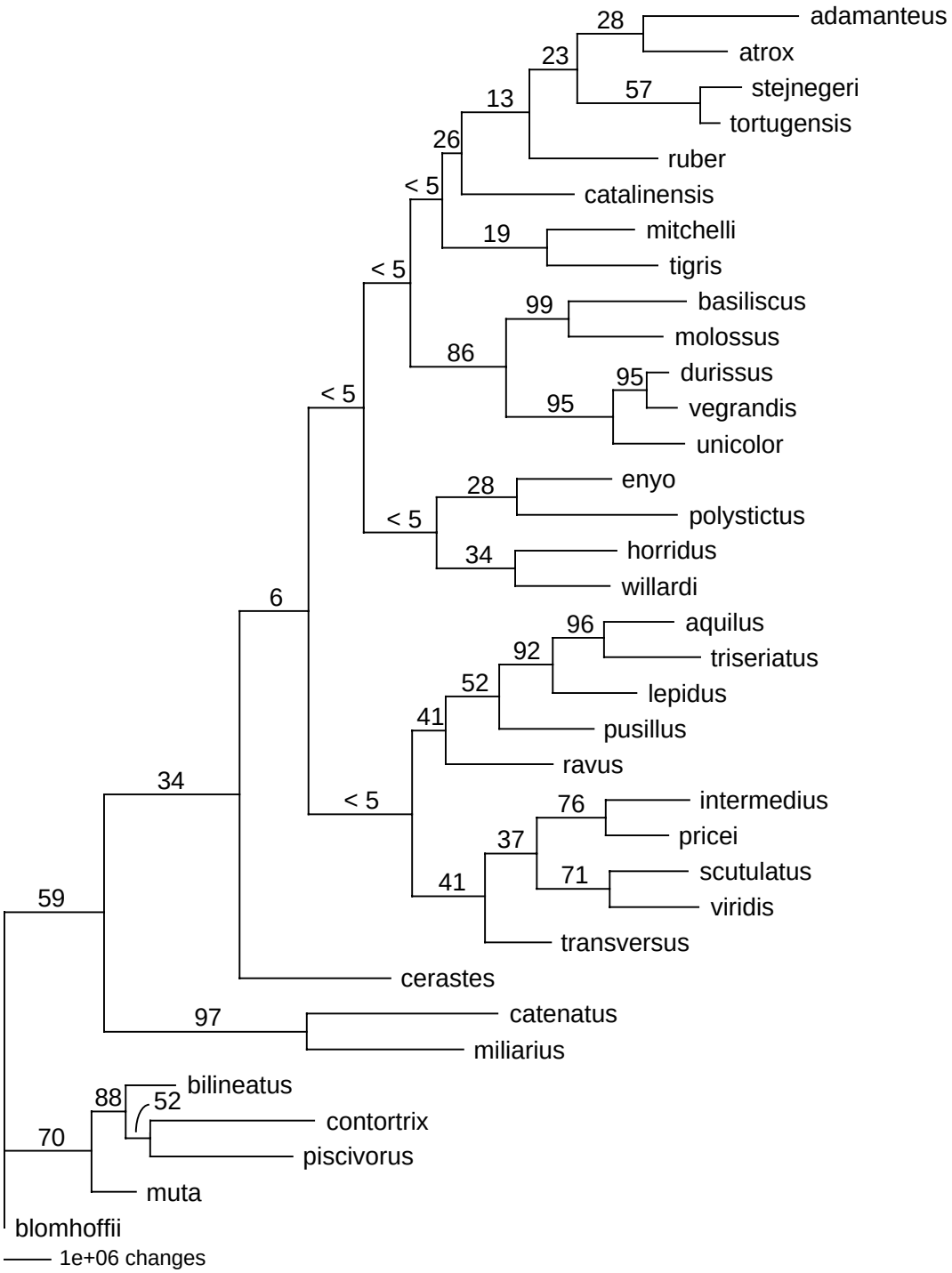


Figure 28. The single most-parsimonious tree found for the rattlesnakes using all available data (combined morphological and molecular data sets) with 96 ambiguously aligned molecular sites included. Numbers above nodes are bootstrap values for support of nodes.

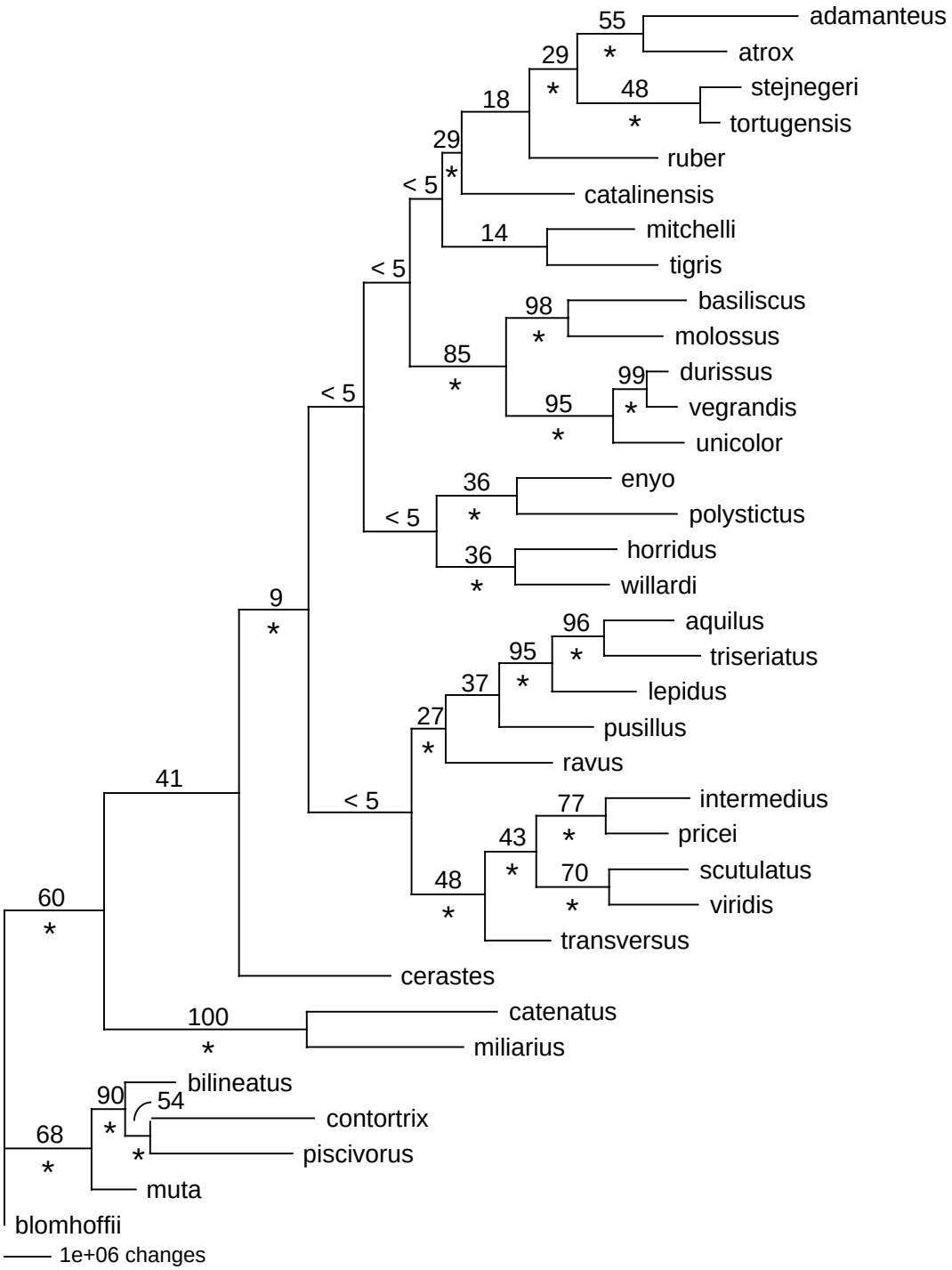


Figure 29. The single most-parsimonious tree found for the rattlesnakes using all available data (combined morphological and molecular data sets) with 96 ambiguously aligned molecular sites excluded. Nodes found in all trees up to one step greater than the most-parsimonious tree are indicated with asterisk (single step between extreme character states equaled 32,767).

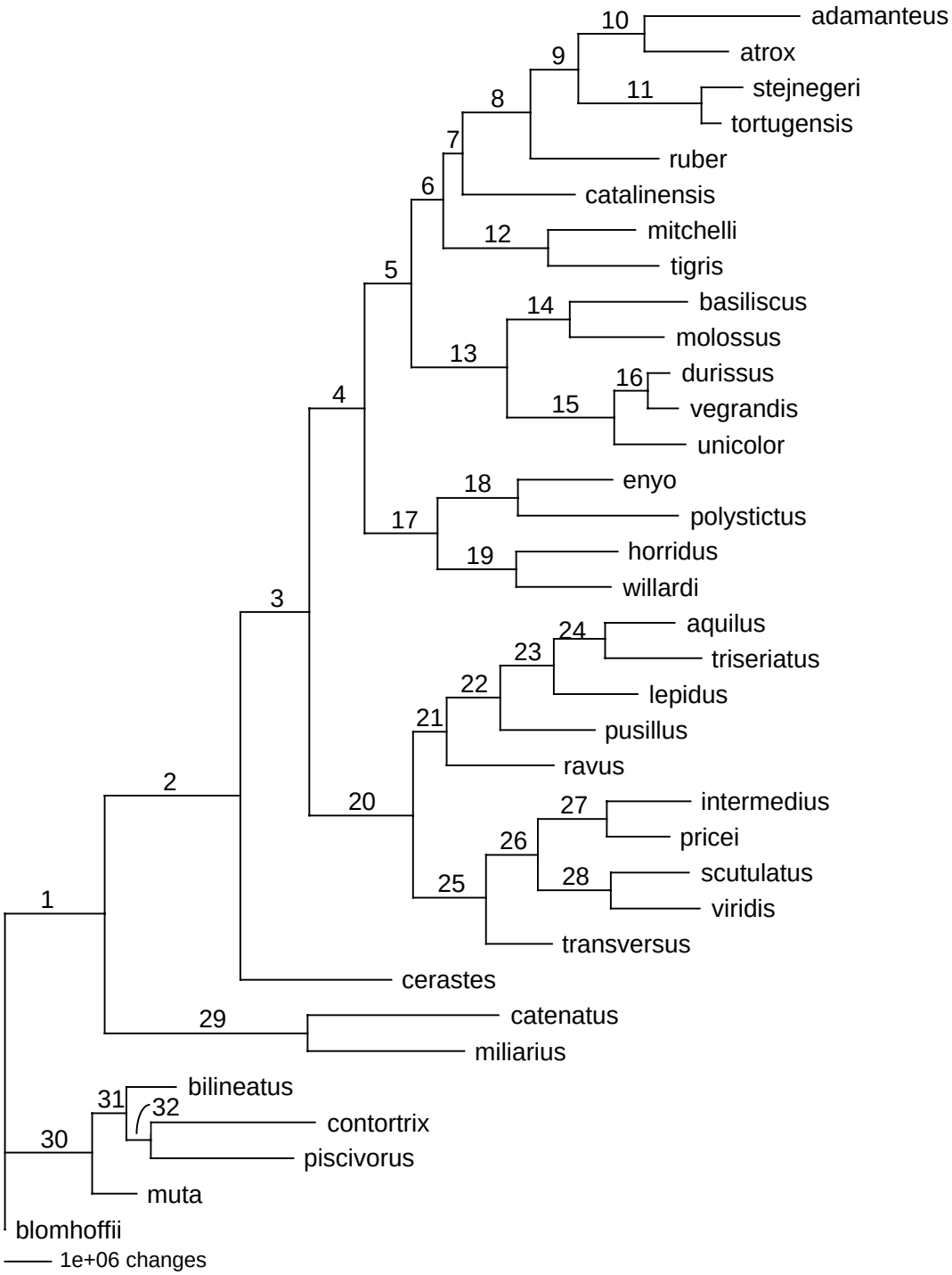


Figure 30. The single most-parsimonious tree found for the rattlesnakes using all available data (combined morphological and molecular data sets) with 96 ambiguously aligned molecular sites excluded. Character state changes supporting the numbered branches are listed in Appendix E.

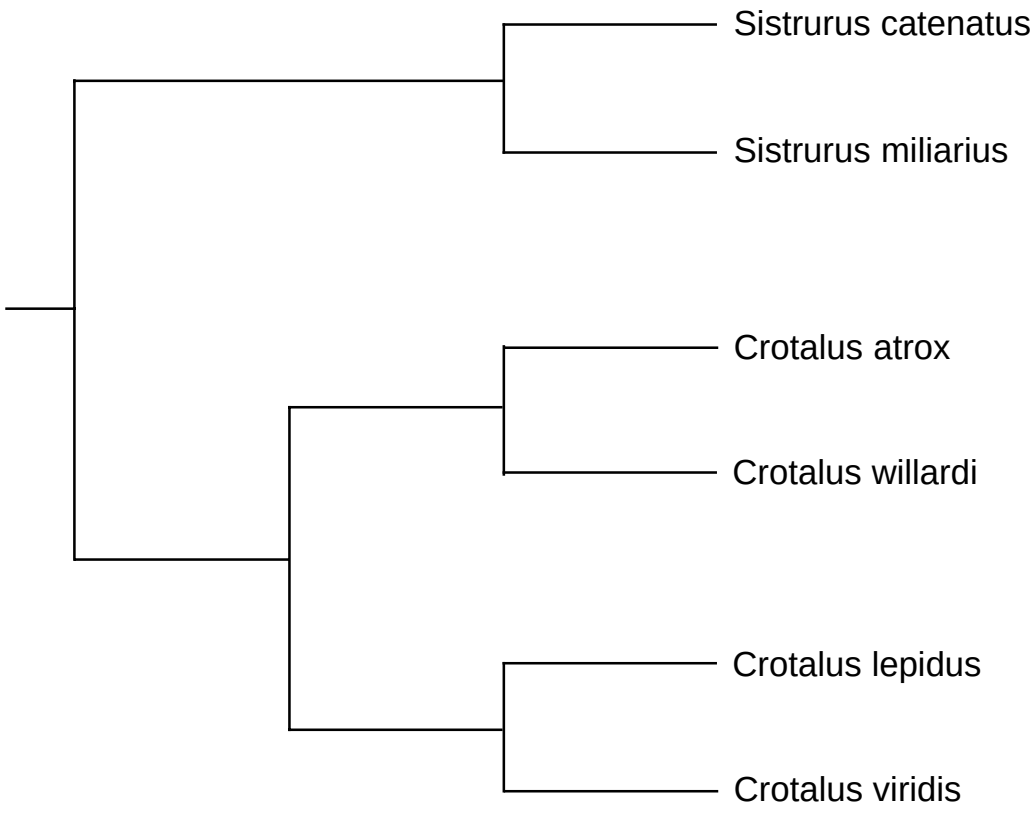


Figure 31. Pruned phylogenetic estimate of rattlesnake relationships estimated from combined data set in Chapter 4 (Figure 29) used for estimating independent contrasts in comparative analyses.

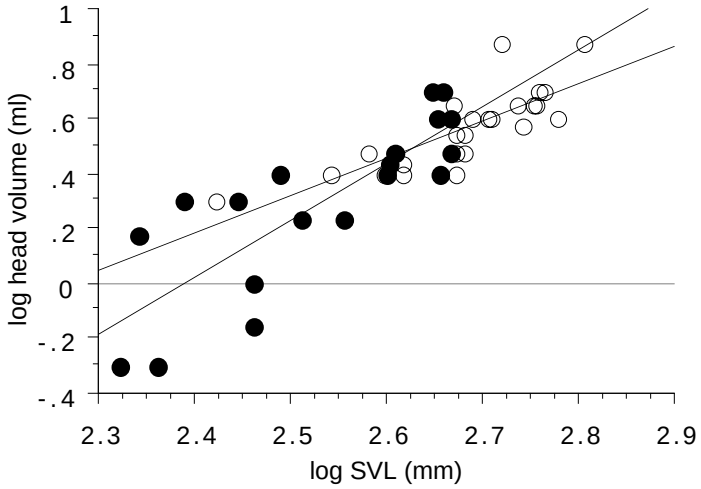


Figure 32. Ordinary least squares regression of log head volume regressed against log snout-vent length in the rock rattlesnake, *Crotalus lepidus*. Females (solid circles): head volume = snout-vent length$^{2.069}$; $r^2 = 0.675$. Males (open circles): head volume = snout-vent length$^{1.355}$; $r^2 = 0.642$.

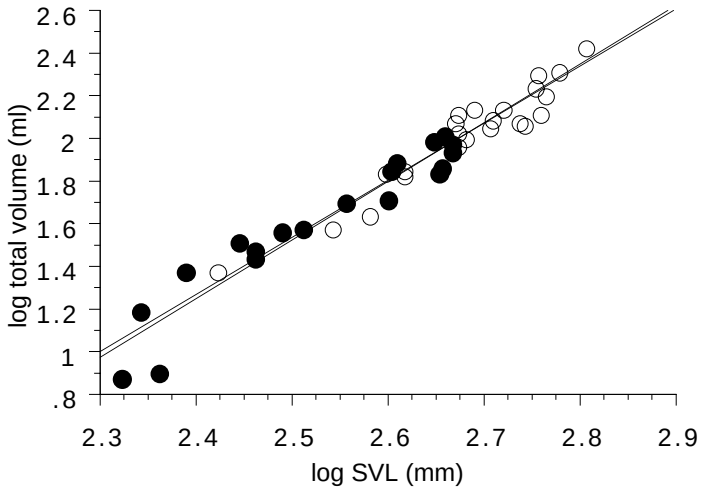


Figure 33. Ordinary least squares regression of log total volume regressed against log snout-vent length in the rock rattlesnake, *Crotalus lepidus*. Females (solid circles): total volume = snout-vent length$^{2.747}$; $r^2 = 0.913$. Males (open circles): total volume = snout-vent length$^{2.682}$; $r^2 = 0.92$.

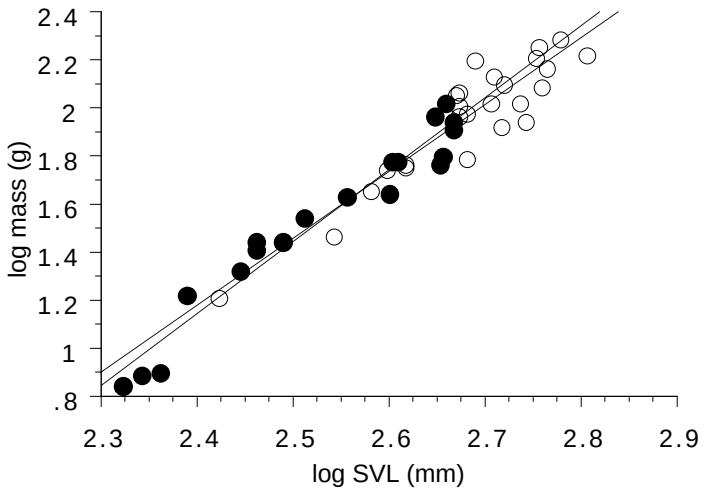


Figure 34. Ordinary least squares regression of log total mass regressed against log snout-vent length in the rock rattlesnake, *Crotalus lepidus*. Females (solid circles): total mass = snout-vent length$^{2.991}$; $r^2 = 0.948$. Males (open circles): total mass = snout-vent length$^{2.787}$; $r^2 = 0.854$.

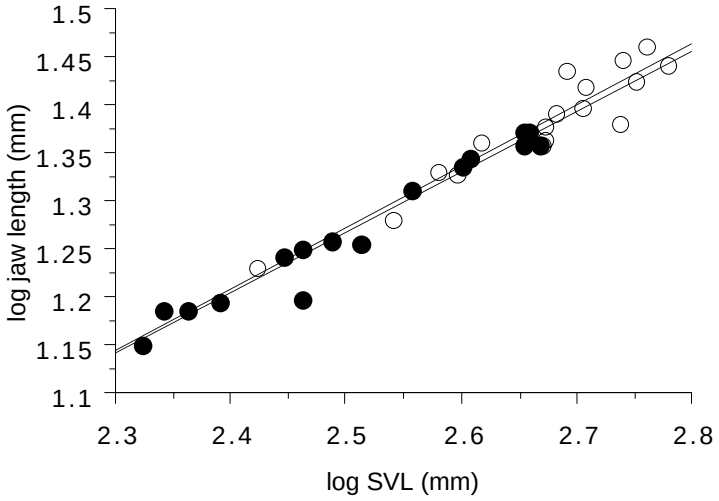


Figure 35. Ordinary least squares regression of log jaw length regressed against log snout-vent length in the rock rattlesnake, *Crotalus lepidus*. Females (solid circles): jaw length = snout-vent length$^{0.638}$; $r^2 = 0.89$. Males (open circles): jaw length = snout-vent length$^{0.628}$; $r^2 = 0.96$.

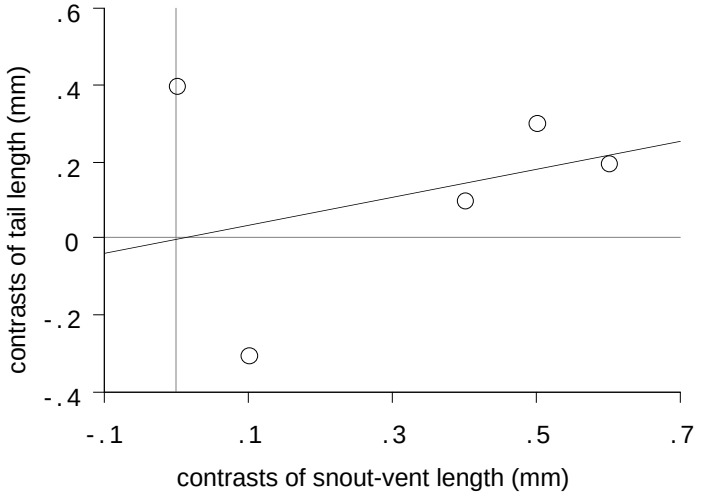


Figure 36. Ordinary least squares regression of tail length (TL) regressed against snout-vent length (SVL). The data are independent contrasts mean values for adult males of six rattlesnake species. Contrasts of tail length = contrasts of snout-vent length$^{0.359}$; r^2 = 0.258.

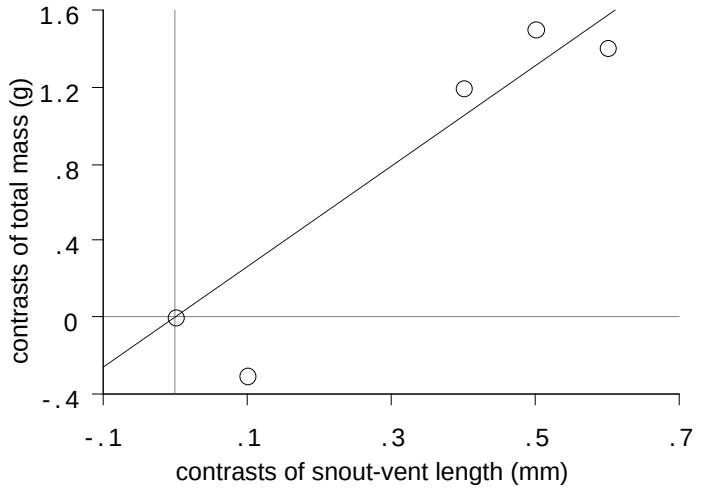


Figure 37. Ordinary least squares regression of total mass regressed against snout-vent length (SVL). The data are independent contrasts mean values for adult males of six rattlesnake species. Contrasts of total mass = contrasts of snout-vent length$^{2.615}$; $r^2 = 0.93$.

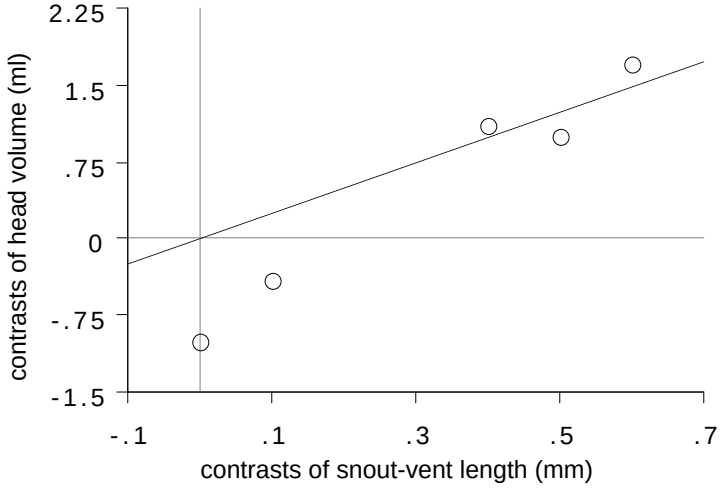


Figure 38. Ordinary least squares regression of head volume regressed against snout-vent length (SVL). The data are independent contrasts mean values for adult males of six rattlesnake species. Contrasts of head volume = contrasts of snout-vent length$^{2.462}$; r^2 = 0.755.

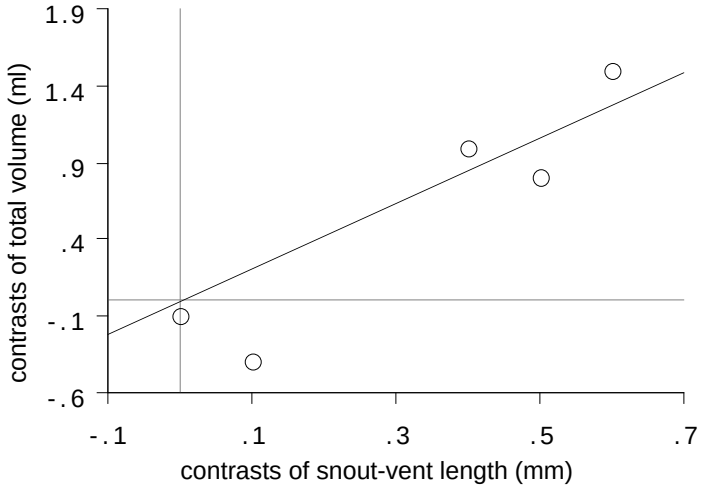


Figure 39. Ordinary least squares regression of total volume regressed against snout-vent length (SVL). The data are independent contrasts mean values for adult males of six rattlesnake species. Contrasts of total volume = contrasts of snout-vent length$^{2.218}$; r^2 = 0.87.

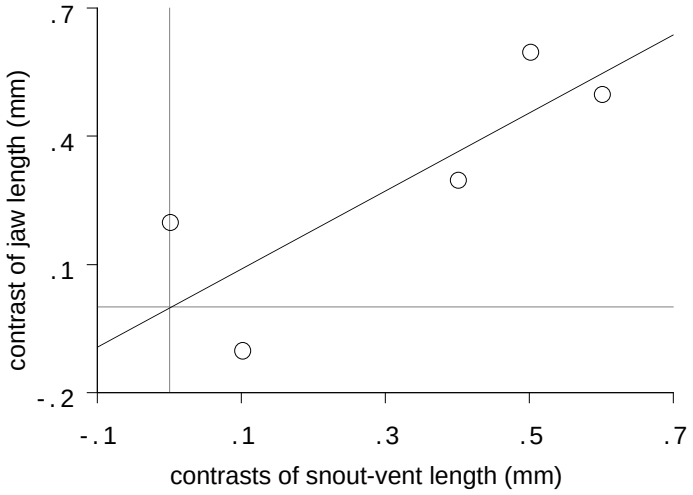


Figure 40. Ordinary least squares regression of jaw length regressed against snout-vent length (SVL). The data are independent contrasts mean values for adult males of six rattlesnake species. Contrasts of jaw length = contrasts of snout-vent length$^{0.91}$; r^2 = 0.862.

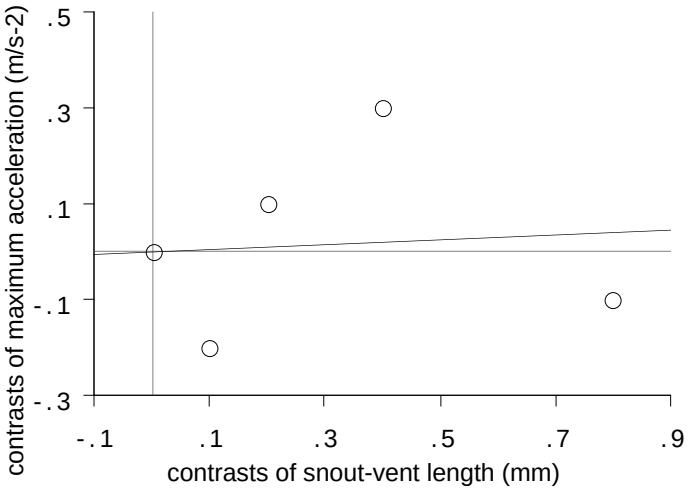


Figure 41. Ordinary least squares regression of maximum acceleration regressed against snout-vent length (SVL). The data are independent contrasts mean values for six rattlesnake species. Contrasts of maximum acceleration = contrasts of snout-vent length$^{0.047}$; $r^2 = 0.013$.

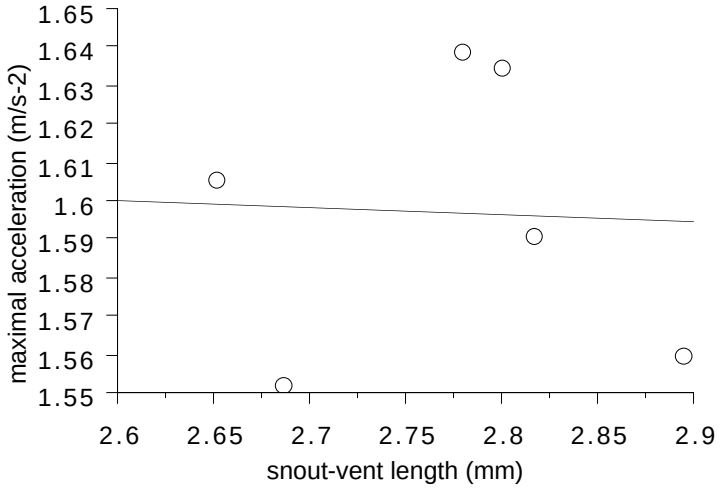


Figure 42. Ordinary least squares regression of maximum acceleration regressed against snout-vent length (SVL). The data are nontransformed mean values for six rattlesnake species. Maximum acceleration = snout-vent length$^{-0.019}$; $r^2 = 0.002$.

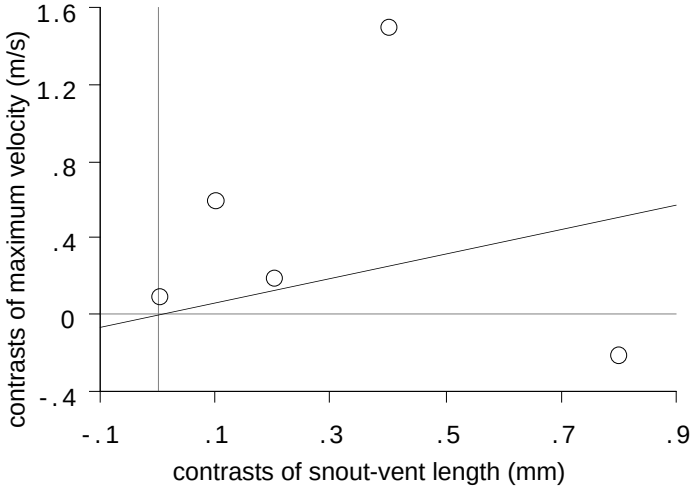


Figure 43. Ordinary least squares regression of maximum velocity regressed against snout-vent length (SVL). The data are independent contrasts mean values for six rattlesnake species. Contrasts of maximum velocity = contrasts of snout-vent length$^{0.635}$; $r^2 = 0.127$.

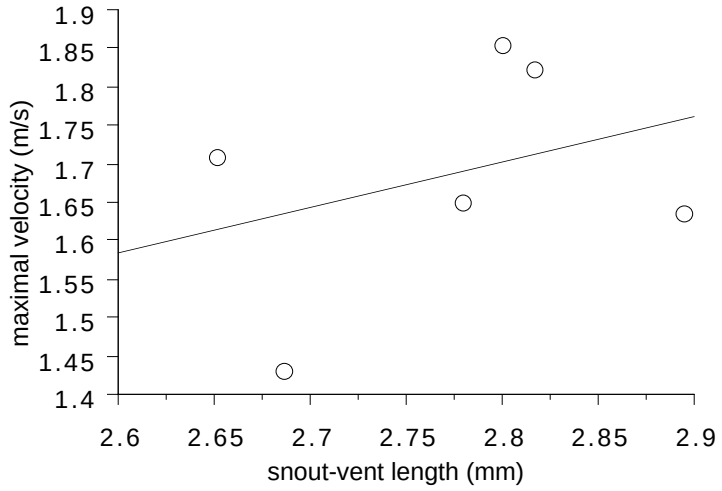


Figure 44. Ordinary least squares regression of maximum velocity regressed against snout-vent length (SVL). The data are nontransformed mean values for six rattlesnake species. Maximum velocity = snout-vent length$^{0.59}$; $r^2 = 0.119$.

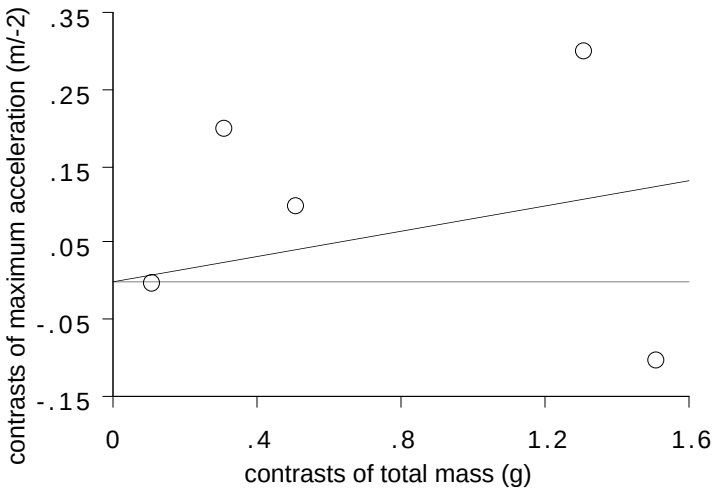


Figure 45. Ordinary least squares regression of maximum acceleration regressed against total mass. The data are independent contrasts mean values for six rattlesnake species. Contrasts of maximum acceleration = contrasts of total mass$^{0.82}$; $r^2 = 0.19$.

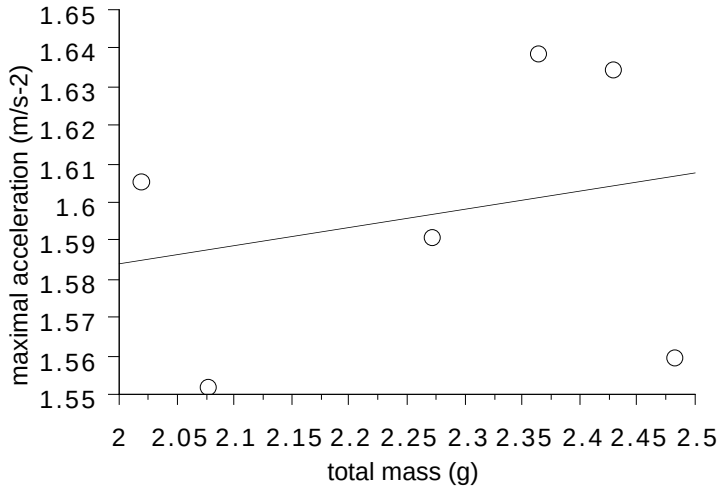


Figure 46. Ordinary least squares regression of maximum acceleration regressed against total mass. The data are nontransformed mean values for six rattlesnake species. Maximum acceleration = total mass$^{0.046}$; $r^2 = 0.058$.

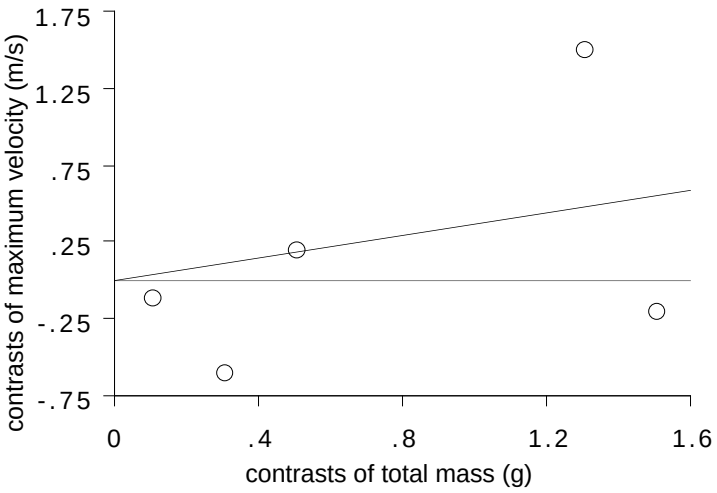


Figure 47. Ordinary least squares regression of maximum velocity regressed against total mass. The data are independent contrasts mean values for six rattlesnake species. Contrasts of maximum velocity = contrasts of total mass$^{0.364}$; $r^2 = 0.21$.

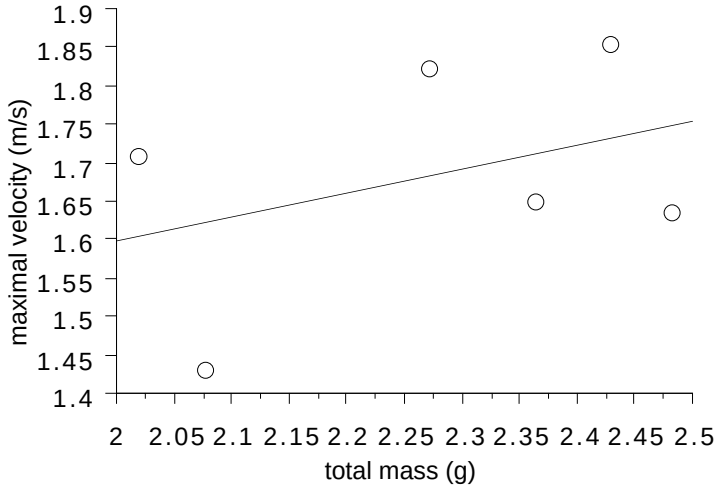


Figure 48. Ordinary least squares regression of maximum velocity regressed against total mass. The data are nontransformed mean values for six rattlesnake species. Maximum velocity = total mass$^{0.313}$; $r^2 = 0.151$.

Appendix A

Specimens examined for intraspecific analyses

Specimens for intraspecific analyses (Chapter 3) were examined from two university collections, Laboratory for Environmental Biology at the University of Texas at El Paso (UTEP) and the Texas Natural History Collection, Texas Memorial Museum at the University of Texas at Austin (TNHC). Specimens with an * were used for both gross morphological measurements and linear cranial measurements, otherwise specimens were only used for gross morphological measurements.

Crotalus atrox: TNHC 3587*, 3708, 3795*, 3796*, 3846*, 4187, 7577, 7648*, 7699*, 7702*, 7756, 7795*, 7801*, 7807*, 7869*, 7870, 7871*, 7889*, 7890*, 7892*, 7934, 7953*, 8000*, 8003, 8024*, 8042*, 8107*, 8117*, 8118*, 8120*, 8221*, 8222*, 8355*, 8571*, 8572*, 9046*, 9047*, 9049*, 9086*, 9087*, 12573*, 12574*, 12605*, 12825*, 12872*, 12933*, 12975*, 14983, 14993*, 17952*, 19641*, 19642*, 19648*, 19806, 19807*, 20261, 20404*, 21616*, 21647*, 21654*, 21743*, 22389, 23079, 23080, 23081, 23082*, 23083*, 23084*, 23085*, 29040*, 29041*, 29042*, 29044*, 29100*, 29101*, 29858*, 29859*, 29861*, 29865*, 29874*, 30447*, 36333*, 42076*, 42256*, 44291*, 44540, 44630, 44631*, 44637*, 47643; UTEP 61, 65, 68, 70, 71, 72, 73, 310, 311, 1063, 1064, 1348, 1486, 1690, 2147, 2148, 2149, 2150, 2151, 2154, 2155, 2156, 2487, 2513, 2654, 3662, 3663, 4370, 5597, 5610, 6111, 6346, 6347, 6359, 8848, 16250.

Appendix B

Specimens examined for phylogenetic analyses

Osteological specimens examined for phylogenetic analyses (Chapter 4). Museum abbreviations follow Leviton et al. (1985) except CJB (private collection of Christopher J. Bell) and TJL (private collection of Travis J. LaDuc). Specimens marked with * indicated disarticulated specimen.

Crotalus adamanteus: CM 36583*, 125900, 125831, 145557*; LSUMZ 29584*, 34173*, 34177*; TCWC 82107. *Crotalus aquilus*: UTACV 4540, 6115, 6179, 9094. *Crotalus atrox*: CJB 1*, 573*, 574*, 577*; CM 112040; LSUMZ 29583*; NAUQSP 6571, 14122; TCWC 81817; UMMZ 175789. *Crotalus basiliscus*: CJB 258; LSUMZ 20499*, 20579; NAUQSP 14086*. *Crotalus catalinensis*: SDNHM 46949*, 59511. *Crotalus cerastes*: CJB 650*, 699*; CM 37565*, 112278, 145577*, 145580*; NAUQSP 14134, 14136; TNHC 35778, 35779. *Crotalus durissus*: CJB 70; LSUMZ 29347*, 55728; NAUQSP 14144; TNHC 35765. *Crotalus enyo*: CJB 1064*, SDNHM 2230*, 46953, 55625; UMMZ 174666, 174667. *Crotalus horridus*: CJB 703*; CM 112009, 125807, 145584*, 145586*, 145590*; LSUMZ 10340*; NAUQSP 14137, 14138, 14142. *Crotalus lepidus*: CJB 1060*, 1061*; NAUQSP 14062; TJL 814*; UMMZ 175800, 175803, 183544*; UTEP-OC 664, 679. *Crotalus mitchellii*: CJB 644*, 645*, 693*, 702; LSUMZ 24379; NAUQSP 7610, 14135*; SDNHM 57140, 62750*, 62238. *Crotalus molossus*: CJB 154*, 643*, 697*; NAUQSP 7610, 14129*; UMMZ 176024, 176025; UTEP-OC 660, 786*, 878. *Crotalus polystictus*: LSUMZ 55366; SDNHM 48503; TCWC 82069; TJL 930*; UTACV 8270; UTEP-OC 946. *Crotalus pricei*: CJB 1058*, 1059*, 1062*; CM 56123, 112358; LSUMZ 35365; UMMZ 150199, 176854. *Crotalus pusillus*: FMNH 37048*. *Crotalus ravus*: UTA 8271; UTEP-OC 959. *Crotalus ruber*: CJB 29, 490*; CM 145602*, 145603*, 145604*; LSUMZ 21210*; NAUQSP 14085, 14149; SDNHM 55309, 57130. *Crotalus scutulatus*: CJB 662*, 663*; CM 145606, 145607*, 145608*; LSUMZ 22111*; SDNHM 46973, 60382; UTEP 11594; UTEP-OC 1048. *Crotalus stenjegeri*: UTACV 10499. *Crotalus tigris*: LSUMMZ 29461; NAUQSP 7381*, 14109*; TJL 886*; UAZ 36664, 36666; UTEP-OC 785. *Crotalus tortugensis*: LSUMZ 55465; SDNHM 42012. *Crotalus triseriatus*: LSUMZ 42125; SDNHM 55307; UTACV 7286, 7398, 12599. *Crotalus unicolor*: SDNHM 55621, 66333-334; TCWC 82054*. *Crotalus vegrandis*: TCWC 82067; UMMZ 193355. *Crotalus viridis*: CJB 227, 306; CM 145621, 145622*, 145623*, 145624*, 145625*; SDNHM 46981; TNHC 57657*, 57902. *Crotalus willardi*: LSUMZ 83787; SDNHM 46986, 60383*; UTACV 40529. *Sistrurus catenatus*: CJB 678*, 691*; CM 14563*, 96233, 112030, 114373, 114391; NAUQSP 14065*, 14078, 14080*. *Sistrurus miliarius*: CJB 682*, 690*; CM 37153, 145633*; NAUQSP 14083*; TNHC 35780; UTACV 39909.

Agkistrodon bilineatus: CJB 149, 692. *Agkistrodon contortrix*: CJB 694*, 715*; NAUQSP 7331*, 8201*, 14076*; TNHC 57972, 58845; UTEP-OC 524, 817.

Agkistrodon piscivorus: CJB 508*, 685*, 705*; NAUQSP 14060, 14068*, 14075*; TJL 539; TNHC 35781. *Gloydius blomhoffii*: CAS 14622, 16097*; FMNH 73969, 73971. *Lachesis muta*: FMNH 31174, 31748-751, 98753; KU 117479.

Bitis gabonica: CJB 471*, 704. *Bitis nasicornis*: UTEP-OC 663. *Bothrops alternatus*: CJB 99*, 462, 463. *Daboia russelii*: CJB 240*, 608; UTEP-OC 562. *Tropidolaemus wagleri*: CJB 223*, 301; TJL 954.

Appendix C

Numbers of GenBank sequences used in phylogenetic analyses

List of taxa and corresponding GenBank accession numbers for sequences of four genes used in the analyses. All sequences were deposited into GenBank in support of Murphy et al. (2002).

	12S	**$tRNA_{val}$**	**16S**	**ND5**
C. adamanteus	AF259255	AF259110	AF259147	AF259218
C. aquilus	AF259232	AF259088	AF259125	AF259200
C. atrox	AF259256	AF259111	AF259148	AF259219
C. basiliscus	AF259244	AF259099	AF259136	AF259209
C. catalinensis	AF259259	AF259114	AF259151	-
C. cerastes	AF259235	AF259091	AF259128	-
C. durissus	AF259248	AF259103	AF259140	AF259212
C. enyo	AF259245	AF259100	AF259137	-
C. horridus	AF259252	AF259107	AF259144	AF259215
C. intermedius	AF259238	AF259094	AF259131	-
C. lepidus	AF259230	AF259086	AF259123	AF259198
C. mitchellii	AF259250	AF259105	AF259142	-
C. molossus	AF259243	AF259098	AF259135	AF259208
C. polystictus	AF259236	AF259092	AF259129	AF259203
C. pricei	AF259237	AF259093	AF259130	AF259204
C. pusillus	AF259229	AF259085	AF259122	AF259197
C. ravus	AF259228	AF259084	AF259121	AF259196
C. ruber	AF259261	AF259116	AF259153	AF259223
C. scutulatus	AF259254	AF259109	AF259146	-
C. tigris	AF259249	AF259104	AF259141	AF259213
C. tortugensis	AF259257	AF259112	AF259149	AF259220
C. transversus	AF259239	-	-	AF259206
C. triseriatus	AF259234	AF259090	AF259127	AF259202
C. unicolor	AF259246	AF259101	AF259138	AF259210
C. vegrandis	AF259247	AF259102	AF259139	AF259211
C. viridis	AF259253	AF259108	AF259145	-
C. willardi	AF259240	AF259095	AF259132	AF259207
S. catenatus	AF259226	AF259082	AF259119	AF259194
S. miliarius	AF259227	AF259083	AF259120	AF259195
A. contortrix	AF259224	AF259080	AF259117	AF259192
A. piscivorus	AF259225	AF259081	AF259118	AF259193

Appendix D

List of characters for phylogenetic analysis

The following is a list of characters used in the construction of the phylogeny. Morphological characters coded using the generalized frequency coding method (GFC) were divided into multiple and separate subcharacters in the data matrix; the corresponding data matrix character numbers (NEXUS) are listed for each morphological character. The method used to code character variation (FB [frequency coding], gap-weighting, GFC, or majority) follows the character state definitions; some characters were invariant or not polymorphic. For each NEXUS character, the weight (w) is listed, as is the character consistency index (CI) on the shortest total-evidence tree. Characters 1-15 from Klauber (1972), with additional information for outgroups and *C. ravus* from Gloyd and Conant (1990), Ernst (1982), McCranie (1988), Solórzano and Cerdas (1986). Most osteological characters listed are new, though some are modified from Gutberlet (1998a) and others.

Molecular sequence data was downloaded from GenBank (Appendix B). DNA characters each had a weight of 32767 (CI values are not given for any sequence data).

1. (NEXUS 1) number of scale rows at midbody. Gap-weighting, (w = 1365, CI = 0.270).
2. (NEXUS 2) number of ventrals in males. Gap-weighting, (w = 1365, CI = 0.238).
3. (NEXUS 3) number of subcaudals in males. Gap-weighting, (w = 1365, CI = 0.324).
4. (NEXUS 4) number of supralabials (one side of head; side counted not known). Gap-weighting, (w = 1365, CI = 0.348).
5. (NEXUS 5) number of infralabials (one side of head; side counted not known). Gap-weighting, (w = 1365, CI = 0.276).
6. (NEXUS 6) number of body blotches, from nape to vent. Gap-weighting, (w = 1365, CI = 0.300).
7. (NEXUS 7) values of body length/head length for adult males. Gap-weighting, (w = 1365, CI = 0.182).
8. (NEXUS 8) width of the proximal rattle/length overall. Gap-weighting, (w = 1365, CI = 0.231).
9. (NEXUS 9) total body length/fang length. Gap-weighting, (w = 1365, CI = 0.212).
10. (NEXUS 10) head length/fang length. Gap-weighting, (w = 1365, CI = 0.258).
11. (NEXUS 11) length of hemipene/diameter of hemipene. Gap-weighting, (w = 1365, CI = 0.343).
12. (NEXUS 12) number of spines per hemipenial lobe. Gap-weighting, (w = 1365, CI = 0.320).
13. (NEXUS 13) number of fringes per hemipenial lobe. Gap-weighting, (w = 1365, CI = 0.343).
14. (NEXUS 14) number of spines in crotch of hemipenes: zero (0); 1-3 (1); >3 (2). Not polymorphic, (w = 32767, CI = 0.182).

15. (NEXUS 15) transition boundary between spines and fringes on hemipenes: gradual (0); intermediate (1); abrupt (2). Not polymorphic, (w = 32767, CI = 0.500).

PALATINE

16. (NEXUS 16-21) number of palatine tooth sockets. GFC, (16:w = 0, CI = 1.000; 17:w = 341, CI = 0.462; 18:w = 341, CI = 0.178; 19:w = 341, CI = 0.400; 20:w = 341, CI = 1.000; 21:w = 0 , CI = 1.000).
17. (NEXUS 22-23) posterior pterygoid process: (0) not forked (or saddled); (1) cupped or saddled; (2) forked or grooved (such that medioposterior and lateroposterior pterygoid processes are separate). GFC, (22:w = 0, CI = 1.000; 23:w = 1365, CI = 0.111).
18. (NEXUS 24) length of palatine: (0) ventral edge approx. twice as long as dorsal height; (1) ventral edge greater than two times as long as dorsal height. FB, (w = 1365, CI = 0.151).
19. (NEXUS 25-26) position of first palatine tooth: (0) anteriormost point, along leading edge; (1) posterior to leading edge, but less than tooth width from leading edge; (2) posterior to leading edge, greater than tooth width from leading edge. GFC, (25:w = 780, CI = 0.255; 26:w = 780, CI = 0.316).
20. (NEXUS 27-32) position of apex of choanal process, relative to teeth: (0) anterior to first socket, (1) above first socket, (2) between first socket and medial socket (or middle of tooth row) (3) above median socket (or middle of tooth row), (4) between median socket (or middle of tooth row) and last socket, (5) above last socket, (6) posterior to last socket [modified from Werman, 1992; Gutberlet, 1998a]. GFC, (27:w = 260, CI = 1.000; 28:w =260 , CI = 0.649; 29:w = 260, CI = 0.444; 30:w = 260, CI = 0.270; 31:w = 260, CI = 0.126; 32:w = 260, CI = 0.222).
21. (NEXUS 33) apex of choanal process: (0) not curved, (1) curved. FB, (w = 1365, CI = 0.145).
22. (NEXUS 34) apex of choanal process: (0) curved medially (piscivorus); (1) curved laterally. FB, (w = 1365, CI = 0.400).
23. (NEXUS 35) apex of choanal process: (0) apex rounded, (1) apex squared. FB, (w = 1365, CI = 0.789).
24. (NEXUS 36) posterior margin of choanal process: (0) concave, (1) straight or convex [modified from Kluge 1993]. FB, (w = 1365, CI = 0.126).

ECTOPTERYGOID

25. (NEXUS 37-38) anterolateral maxillary process: (0) lateral edge without blunt, straight vertical face; (1) lateral edge with 45° straight face; (2) lateral edge with blunt, straight vertical (90°) face. GFC, (37:w = 683, CI = 0.245; 38:w = 683, CI = 0.545).
26. (NEXUS 39-40) anterolateral maxillary process: (0) ventrolateral surface smooth or weakly convex; (1) ventrolateral surface weakly concave; (2) ventrolateral surface deeply concave. GFC, (39:w = 683, CI = 0.141; 40:w = 683, CI = 0.203).

27. (NEXUS 41-42) anteromedial maxillary process (including portion of articulating facet between two processes): (0) greater than 1/3 facet width; (1) facet height 1/3 facet width; (2) facet height less than 1/3 facet width. GFC, (41:w = 1365, CI = 0.136; 42:w = 0, CI = 1.000).
28. (NEXUS 43-44) anteromedial maxillary process: (0) dorsomedial surface smooth or weakly convex; (1) dorsomedial surface weakly concave; (2) dorsomedial surface deeply concave. GFC, (43:w = 683, CI = 0.145; 44:w = 683, CI = 0.136).
29. (NEXUS 45-46) anterior maxillary processes, in reference to hypothetical line perpendicular to medial edge of shaft: (0) both processes extend equal distances anteriorly; (1) anterolateral process extends only slightly farther anteriorly; (2) anterolateral process extends at least twice as far anteriorly. GFC, (45:w = 683, CI = 0.119; 46:w = 683, CI = 0.157).
30. (NEXUS 47) facets for articulation with pterygoid: (0) area of contact between is relatively simple, flat or composed of no more than one convex-concave facet; (1) complex, consisting of two or more such facets. Not polymorphic, (w = 32767, CI = 1.000).
31. (NEXUS 48) curvature in the anterior edge between anterior maxillary processes: (0) ~90 degree angle on both sides; (1) ~90 degree angle on lateral edge only; (2) ~90 degree angle on medial edge only; (3) neither edge with ~90 degree angle. Majority, (w = 32767, CI = 0.333)
32. (NEXUS 49) length of ectopterygoid: (0) shorter; (1) longer than base of pterygoid (posterior to articulation with ectopterygoid) [modified from Gutberlet, 1998a; also mentioned by Brattstrom,1964]. FB, (w = 1365, CI = 0.205).

PTERYGOID

33. (NEXUS 50-62) number of pterygoid teeth sockets. GFC, (50:w = 115, CI = 0.480, 51:w = 115, CI = 0.171, 52:w =115, CI = 0.122, 53:w = 115, CI = 0.179, 54:w = 115, CI = 0.571, 55:w = 115, CI = 0.522, 56:w = 115, CI = 0.571, 57:w = 115, CI = 0.667, 58:w = 115, CI = 0.667, 59:w = 115, CI = 0.750, 60:w = 115, CI = 0.870, 61:w = 115, CI = 1.000; 62:w =115, CI = 0.750).
34. (NEXUS 63-64) placement of teeth: (0) teeth only found anterior to articulation of ectopterygoid; (1) tooth row ends within region of articulation with ectopterygoid; (2) tooth row ends posterior to articulation of ectopterygoid. GFC, (63:w = 910 , CI = 0.429; 64:w = 910, CI = 0.545).
35. (NEXUS 65) articulation of ectopterygoid: (0) within curvature of lateral edge; (1) anterior of lateral edge curvature. FB, (w = 1365, CI = 0.211).
36. (NEXUS 66-67) presence of notch on posteromedial edge for articulation with ectopterygoid: (0) absent; (1) present, but weak (adamanteus); (2) present, with two large bony projections. GFC, (66:w = 683, CI = 0.282; 67:w = 683, CI = 1.000).
37. (NEXUS 68) pterygoid: (0) no dorsal concavity formed by lateral ridge; (1) small dorsal concavity formed by lateral ridge. Invariant, (w = 1365, CI = 1.000)
38. (NEXUS 69) lateral and medial curvature, moving posteriorly: (0) lateral edge curves before medial edge; (1) both edges curve at same point. FB, (w = 1365, CI = 0.235).

39. (NEXUS 70) presence of foramen at anterior end of lateral ventral fossa: (0) absent; (1) present, either inside fossa or just anterior to fossa on lateral edge. FB, (w = 1365, CI = 0.222).
40. (NEXUS 71) presence of nutritive foramen at posterior end of tooth row on ventral surface (enclosed within the bone, not within sockets): (0) absent; (1) present. FB, (w = 1365, CI = 0.140).
41. (NEXUS 72-73) position of nutritive foramen at posterior end of tooth row on ventral surface (enclosed within the bone, not within sockets): (0) lateral to last or penultimate tooth; (1) posterior to last tooth. GFC, (72:w = 1365, CI = 0.667; 73:w = 0, CI = 1.000).
42. (NEXUS 74-75) articulation point with palatine, anterior edge of bone: (0) no notch in anterior edge; (1) weakly notched; (2) strongly notched. GFC, (74:w = 964, CI = 0.429; 75:w = 964, CI = 0.103).
43. (NEXUS 76) presence of small convex humps on posterior lateral edge: (0) absent, lateral edge straight; (1) present, at least one hump present near ectopterygoid articulation. FB, (w = 1365, CI = 0.202).

MAXILLA

44. (NEXUS 77) shape of V_2p foramen, internally on lateral face of pit wall: (0) egg shaped, narrow dorsally (twice as high as wide); (1) rounded, not egg-shaped (not twice as high as wide, roughly equal measures). FB, (w = 1365, CI = 0.168).
45. (NEXUS 78) dorsal prefrontal process: (0) posterodorsal surface roughly as wide as high; (1) posterodorsal surface wider than high [modified from Holman, 1959]. FB, (w = 1365, CI = 0.414).
46. (NEXUS 79) dorsal prefrontal process: (0) entire dorsal edge rounded; (1) medial portion of dorsal edge straight. FB, (w = 1365, CI = 0.129).
47. (NEXUS 80) dorsal prefrontal process: (0) ventral edge straight; (1) ventral edge curves ventrally, concavity in lower edge at contact with medial edge. FB, (w = 1365, CI = 0.126).
48. (NEXUS 81) process on anteromedial wall process: (0) knob absent; (1) knob present. FB, (w = 1365, CI = 0.750).
49. (NEXUS 82) direction of projecting anteromedial wall process: (0) laterally projecting; (1) anteriorly projecting. FB, (w = 1365, CI = 0.522).

DENTARY

50. (NEXUS 83-93) number of dentary tooth sockets. GFC, (83:w = 134, CI = 0.667; 84:w = 134, CI = 0.150; 85:w = 134, CI = 0.124; 86:w = 134, CI = 0.233; 87:w = 134, CI = 0.667; 88:w = 134, CI = 1.000; 89:w = 134, CI = 1.000; 90:w = 134, CI = 1.000; 91:w = 134, CI = 0.750; 92:w = 134, CI = 0.750; 93:w = 134, CI = 1.000).
51. (NEXUS 94) presence of foramen on medial surface: (0) absent; (1) present. FB, (w = 1365, CI = 0.276).

52. (NEXUS 95) position of foramen on medial surface: (0) anterior position, under first three tooth sockets; (1) posterior position, caudal to first three tooth sockets. FB, (w = 1365, CI = 0.146).
53. (NEXUS 96) longest articular process: (0) ventral; (1) dorsal. Not polymorphic, (w = 32767, CI = 0.500).
54. (NEXUS 97-98) dorsal articular process: (0) lateral fork longer than medial fork; (1) both lateral and medial forks equal length; (2) medial fork longer than lateral fork. GFC, (97:w = 683, CI = 0.150; 98:w = 683, CI = 0.207).
55. (NEXUS 99) dentary teeth: (0) posteriormost teeth anterior to angular; (1) posteriormost teeth dorsal to angular. FB, (w = 1365, CI = 0.558).

ANGULAR/SPLENIAL

56. (NEXUS 100-101) angular and splenial: (0) separate; (1) partially fused; (2) completely fused [modified from Gutberlet, 1998a] GFC, (100:w = 683, CI = 0.178; 101:w = 683, CI = 0.216).
57. (NEXUS 102-103) splenial: (0) no additional foramen enclosed within splenial; (1) dorsal edge of splenial, forming ventral edge of Meckelian foramen, with small process indicating partial separation of foramen; (2) separate foramen entirely enclosed within splenial, below Meckelian foramen [Gutberlet, 1998a]. GFC, (102:w = 840, CI = 0.118; 103:w = 840, CI = 0.283).
58. (NEXUS 104) Meckelian foramen: (0) angular borders approximately one half of posterior margin of foramen; (1) angular excluded or almost excluded (less than 1/4 posterior margin) from foramen margin by anterior projection of splenial. FB, (w = 1365, CI = 0.179).
59. (NEXUS 105) splenial: (0) splenial attenuate anteriorly, groove in dentary open medially; (1) splenial not attenuate anteriorly, contacts dentary to cover portion of groove (Meckelian foramen enclosed on three sides by splenial). FB, (w = 1365, CI = 0.308).

ARTICULAR

60. (NEXUS 106) ventrolateral process: (0) absent; (1) thin ventrolateral process below level of the junction with the quadrate. FB, (w = 1365, CI = 0.143).
61. (NEXUS 107) position of anterior articular foramen: (0) anterior to anteriormost extension of the dorsal projection; (1) posterior to anteriormost extension of the dorsal projection. Invariant, (w = 32767, CI = 1.000).
62. (NEXUS 108) posterior Meckelian foramen: (0) foramen visible from dorsal view; (1) foramen not visible from dorsal view. FB, (w = 1365, CI = 0.118).
63. (NEXUS 109) medial process ventral to quadrate articulation: (0) absent; (1) present. FB, (w = 1365, CI = 0.308).
64. (NEXUS 110-111) shape of medial process ventral to quadrate articulation: (0) small rounded bump; (1) small pointed projection; (2) distinct pointed anteromedial process. GFC, (110:w = 683, CI = 0.147; 111:w = 683, CI = 0.168).

QUADRATE

65. (NEXUS 112) quadrate, shape of posterior process: (0) not forked; (1) forked. Invariant, (w = 32767, CI = 1.000).
66. (NEXUS 113) shape of anterior half: (0) first 1/3 equal width, with thin lateral processes off of each side of bone, only narrows at intercalary nodule; (1) first 1/3 narrows well before intercalary nodule, without thin lateral processes. FB, (w = 1365, CI = 0.113).
67. (NEXUS 114) anterior margin: (0) rounded; (1) squared off. FB, (w = 1365, CI = 0.142).
68. (NEXUS 115) lateral margin: (0) edge mostly straight, not bowed dorsally; (1) edge rounded, bowed dorsally. FB, (w = 1365, CI = 0.132).
69. (NEXUS 116) anterior end: (0) dorsal surface relatively flat; (1) dorsal surface concave. FB, (w = 1365, CI = 0.152).
70. (NEXUS 117-118) posterior end: (0) dorsal surface relatively flat proximal to articulation facet; (1) dorsal surface shallowly concave proximal to articulation facet; (2) dorsal surface deeply concave proximal to articulation facet. GFC, (117:w = 1092, CI = 0.112; 118:w = 840, CI = 0.375).
71. (NEXUS 119) length: (0) shorter than ectopterygoid; (1) equal to or longer than ectopterygoid. FB, (w = 1365, CI = 0.400).

SUPRATEMPORAL

72. (NEXUS 120) supratemporal: (0) caudal end widened but lacking distinct projection; (1) caudal end widened with posterolateral projection. FB, (w = 1365, CI = 0.750).
73. (NEXUS 121) supratemporal, posterolateral projection: (0) small; (1) large [modified from Werman 1992; Gutberlet, 1998a]. FB, (w = 1365, CI = 0.123).
74. (NEXUS 122) posterolateral process: (0) rounded; (1) pointed; (2) squared. Majority, (w = 32767, CI = 1.000).
75. (NEXUS 123) medial margin: (0) without definite concavity between posteromedial process and anterior process; (1) with definite concavity between posteromedial process and anterior process. FB, (w = 1365, CI = 0.153).
76. (NEXUS 124) lateral margin: (0) margin mostly straight, slight concavity; (1) margin concave, anterior process crescent shaped. FB, (w = 1365, CI = 0.161).
77. (NEXUS 125) anterior process: (0) posterior base of anterior process equal to or wider than anterior end; (1) posterior base of anterior process narrower than anterior end. FB, (w = 1365, CI = 0.183).
78. (NEXUS 126) posterior processes: (0) no distinct process, either lateral or medial; (1) at least one distinct process, whether lateral or medial or both. FB, (w = 1365, CI = 1.000).
79. (NEXUS 127-128) posterior processes: (0) only lateral distinct; (1) both medial and lateral processes distinct; (2) only medial distinct (caused by concavities in medial, lateral and posterior margins). GFC, (127:w = 1092, CI = 0.138; 128:w = 1092, CI = 0.429).

80. (NEXUS 129) supratemporal: (0 with a rounded dorsal surface; (1) with a flat dorsal surface [modified from Gutberlet, 1998a]. FB, (w = 1365, CI = 0.163).
81. (NEXUS 130) length: (0) greater than 50% quadrate length; (1) less than or equal to 50% quadrate length. FB, (w = 1365, CI = 0.828).
82. (NEXUS 131) amount of concavity in bone: (0) all three processes contact ground or lateral just barely losing contact when placed on flat surface; (1) lateral process points upward when placed on flat surface. FB, (w = 1365, CI = 0.240).

PREMAXILLA

83. (NEXUS 132-133) anterior edge of transverse bar: (0) anterior edge (middle 1/3) of the transverse bar concave; (1) anterior edge (middle 1/3) of the transverse bar (seen from above) straight; (2) convex. GFC, (132:w = 780, CI = 0.692; 133:w = 780, CI = 0.230).
84. (NEXUS 134-135) posterior margin of ventral edge, exclusive of palatal processes: (0) smooth, no point or process along length of margin; (1) low bump, not distinct processes; (2) distinct small posterior processes. GFC, (134:w = 683, CI = 0.147; 135:w = 683, CI = 0.153).
85. (NEXUS 136) posterior margin: (0) nearly perpendicular to the midline; (1) slopes posteriorly [modified from Kluge, 1993]. FB, (w = 1365, CI = 0.119).
86. (NEXUS 137) dorsal margin of anterior edge: (0) without pair of small dorsal processes adjacent to ascending process; (1) pair of small dorsal processes, on either side and lateral to ascending process. FB, (w = 1365, CI = 0.316).
87. (NEXUS 138) two separate posterior projecting processes of median palatal process: (0) absent; (1) present. FB, (w = 1365, CI = 0.333).
88. (NEXUS 139) separate posterior projecting processes of median palatal process (0) pointed; (1) rounded; (2) lobed; (3) squared. Majority, (w = 32767, CI= 0.250).
89. (NEXUS 140-141) median palatal process: (0) paired processes absent or indistinct from one another; (1) small but separated; (2) large, very distinct. GFC, (140:w = 683, CI = 0.571; 141:w = 683, CI = 0.130).
90. (NEXUS 142) median palatal process: (0) shared horizontal plate does not extend posteriorly from posterior margin of transverse processes; (1) shared horizontal plate extends posteriorly from posterior margin of transverse processes. FB, (w = 1365, CI = 0.400).
91. (NEXUS 143) median fenestra on ventral surface of transverse bar: (0) absent; (1) present [modified from Kluge 1993]. FB, (w = 1365, CI = 0.148).
92. (NEXUS 144) anterior edge of ascending process of premaxilla: (0) narrows as it ascends posteriorly; (1) does not narrow as it ascends posteriorly, maintains same width. FB, (w = 1365, CI = 0.205).
93. (NEXUS 145) ascending process of premaxilla: (0) lateral shelves not present; (1) lateral shelves extend from posterior surface of ascending process dorsal to transverse processes. FB, (w = 1365, CI = 0.261).
94. (NEXUS 146) ascending process of premaxilla: (0) does not extend posterior to posterodorsal margin of processus nasalis; (1) does extend posterior to posterodorsal

margin (if present, forms notch between process and posterior margin of processus nasalis). FB, (w = 1365, CI = 0.137).

NASAL

95. (NEXUS 147) shape of horizontal dorsal shelf: (0) triangular; (1) not triangular. FB, (w = 1365, CI = 0.235).
96. (NEXUS 148) horizontal shelf (not including small anteromedial point, if present): (0) narrower anteriorly; (1) narrower posteriorly. FB, (w = 1365, CI = 0.173).
97. (NEXUS 149) horizontal shelf, length vs. width: (0) longer than wide; (1) wider than long. FB, (w = 1365, CI = 0.198).
98. (NEXUS 150) lateral margin of horizontal shelf: (0) emarginated or with projection(s); (1) smooth. FB, (w = 1365, CI = 0.134).
99. (NEXUS 151-152) anterior projection from ventral edge of median (vertical) shelf formed by anterocaudal constriction of vertical shelf: (0) absent; (1) small projection present (small rounded bump); (2) large projection present. GFC, (151:w = 683, CI = 0.140; 152:w = 683, CI = 0.205).
100. (NEXUS 153-154) ventral edge: (0) not all in same horizontal plane, anterior portion may be slightly elevated/dorsal; (1) entire edge in same horizontal plane (2) not all in same horizontal plane, anterior portion may be slightly depressed/ventral. GFC, (153:w = 964, CI = 0.138; 154:w = 964, CI = 0.310).

VOMER

101. (NEXUS 155) small pointed ventral process on ventral margin of fenestra vomeronasal externa [modified from Groombridge, 1979]: (0) absent; (1) present. FB, (w = 1365, CI = 0.432).
102. (NEXUS 156) small process on inner anteroventral margin of fenestra vomeronasal externa: (0) absent; (1) present. (disarticulated only). FB, (w = 1365, CI = 0.517).
103. (NEXUS 157) anterodorsal process, distal portion in dorsal view: (0) thin, finger-like narrow process (process reduced to thin compressed plate of bone, more laterally compressed than dorsoventrally); (1) triangular process, not finger-like, but dorsoventrally flattened, continuation of broad surface of bone anterior of vomeronasal foramen. FB, (w = 1365, CI = 0.141).
104. (NEXUS 158) posterior and ventral vertical laminae: (0) two laminae share large portion of vertical shelf - shelf extends more than half the distance to the distal tip of the posterior lamina; (1) two laminae do not share large portion of vertical shelf - shelf does not extend more than half the distance to the distal tip of the posterior lamina. FB, (w = 1365, CI = 0.123).
105. (NEXUS 159) posterior and ventral vertical laminae, distal tips: (0) posterior tip extends further caudally; (1) tips equidistant caudally. FB, (w = 1365, CI = 0.264).
106. (NEXUS 160) posterior and ventral vertical laminae, margin between: (0) not U-shaped; (1) U-shaped. FB, (w = 1365, CI = 0.140).
107. (NEXUS 161) posterior vertical lamina, distal end: (0) entire, not notched or forked; (1) forked or notched. FB, (w = 1365, CI = 0.188).

108. (NEXUS 162) posterior vertical lamina, length (from posterior edge of concave bone housing Jacobson's organ to distal tip of lamina): (0) less than height of vomer, from dorsal margin to distal tip of ventral vertical lamina; (1) greater than or equal to height of vomer. FB, (w = 1365, CI = 0.166).
109. (NEXUS 163) ventral vertical lamina foramen/foramina: (0) absent; (1) present. FB, (w = 1365, CI = 0.500).

SEPTOMAXILLA

110. (NEXUS 164) dorsoposterior process: (0) in lateral view, constricted at proximal connection with rest of bone in that constriction narrower than largest width on process; (1) proximal connection not constricted in lateral view, attachment is widest point. FB, (w = 1365, CI = 0.308).
111. (NEXUS 165) dorsoposterior process: (0) process terminates as rounded lamina; (1) tapers into narrow and pointed lamina. FB, (w = 1365, CI = 0.632).
112. (NEXUS 166) orientation of narrow and pointed dorsoposterior process: (0) vertical lamina;(1) horizontal lamina. FB, (w = 1365, CI = 0.308).
113. (NEXUS 167) dorsoposterior process, length: (0) shorter than body of septomaxilla; (1) longer than or equal to body of septomaxilla. FB, (w = 1365, CI = 0.134).
114. (NEXUS 168) dorsolateral process: (0) process laterally compressed with rounded edges, center of process without medially angled thickened knob; (1) center of process with medially angled thickened knob, and with thin delicate curving process on distal tip. FB, (w = 1365, CI = 1.000).
115. (NEXUS 169) presence of small distinct projection (ventral) along posterolateral margin of septomaxilla that roofs vomeronasal fenestra (hidden in articulated specimens): (0) absent; (1) present. FB, (w = 1365, CI = 0.148).
116. (NEXUS 170) anteromediodorsal margin, corner: (0) in same horizontal plane as dorsal edge of posterodorsal process; (1) not in same straight horizontal plane as dorsal edge of posterodorsal process. FB, (w = 1365, CI = 0.113).
117. (NEXUS 171-172) anterior edge of septomaxilla: (0) asymmetry in leading edge as medial portion of anterior margin extends further anteriorly than rest of margin; (1) no asymmetry in leading edge, may have one or more lobes (may be of different sizes) but all extending equal distance anterior; (2) asymmetry in leading edge as lateral portion of anterior margin extends further anteriorly than rest of margin. GFC, (171:w = 683, CI = 0.166; 172:w = 683, CI = 0.706).

PREFRONTAL

118. (NEXUS 173) posterolateral processes: (0) middle and ventral processes equal in length; (1) middle process longer than ventral process. FB, (w = 1365, CI = 0.316).
119. (NEXUS 174) posterolateral processes: (0) dorsal and ventral processes extend equal lengths caudally; (1) ventral process extends further caudally than dorsal process. FB, (w = 1365, CI = 0.273).
120. (NEXUS 175) posterolateral processes: (0) middle and ventral processes not fused; (1) middle and ventral processes fused. FB, (w = 1365, CI = 0.194).

121. (NEXUS 176) ventral posterolateral process: (0) without medial projection; (1) with medial projection. FB, (w = 1365, CI = 0.429).
122. (NEXUS 177-178) posterodorsolateral process: (0) equal height as anterodorsolateral process; (1) slightly higher than anterodorsolateral process; (2) twice as high or higher than anterodorsolateral process. GFC, (177:w = 683, CI = 0.150; 178:w = 683, CI = 0.203).
123. (NEXUS 179) projection on anteroventrolateral surface, causing anterolateral surface concavity: (0) absent; (1) lateral or ventral projection present. FB, (w = 1365, CI = 0.149).
124. (NEXUS 180) foramen in anterolateral wall, in concavity: (0) absent; (1) present. FB, (w = 1365, CI = 0.130).
125. (NEXUS 181) medial margin, between anteromedial and posteromedial corners: (0) not concave; (1) concave. FB, (w = 1365, CI = 0.203).
126. (NEXUS 182) anteromedial wing: (0) absent; (1) present. FB, (w = 1365, CI = 0.112).
127. (NEXUS 183) shape of anteromedial wing: (0) low bump; (1) raised anterior margin of lacrimal foramen; (2) distinct process. Majority, (w = 32767, CI = 0.500).
128. (NEXUS 184) posterior margin: (0) mostly straight, with slight posterior bulge at posterodorsolateral corner; (1) 2/3 of border straight, large posterior bulge at posterodorsolateral corner, ~ 90 degree angle between posterior edge and bulge. FB, (w = 1365, CI = 0.429).
129. (NEXUS 185) prefrontal: (0) entire bone not bent, in horizontal plane; (1) entire bone bent: medial half of bone more horizontal, lateral half of bone more vertical. FB, (w = 1365, CI = 0.632).

FRONTAL

130. (NEXUS 186-198) frontal shape, ratio [measured along midline of each axis] – length/width ratio divided into bins 0.1 (0.9 – 2.2). GFC, (186:w = 137, CI = 0.538; 187:w = 137, CI = 0.333; 188:w = 137, CI = 0.136; 189:w = 137, CI = 0.154; 190:w = 137, CI = 0.150; 191:w = 137, CI = 0.160; 192:w = 137, CI = 0.253; 193:w = 137, CI = 0.282; 194:w = 137, CI = 0.316; 195:w = 137, CI = 0.310; 196:w = 137, CI = 0.484; 197:w = 137, CI = 0.600; 198:w = 0, CI = 1.000).
131. (NEXUS 199) frontal, lateral margin: (0) flat; (1) elevated [modified from Gutberlet, 1998a]. FB, (w = 1365, CI = 1.000).
132. (NEXUS 200) frontal, anterior margin: (0) flat; (1) lateral anterior margin elevated. FB, (w = 1365, CI = 0.769).
133. (NEXUS 201) frontal, anterior margin: (0) medial corner not markedly anterior of center of anterior margin - medial half of anterior margin not concave; (1) medial corner marked anterior of center of anterior margin - medial half of anterior margin concave. FB, (w = 1365, CI = 0.200).
134. (NEXUS 202-205) anterior and posterior lateral corners, ratio: posterior width (to lateral corner)/anterior width (to lateral corner). Divided into bins 0.1 (0.6 – 1.0).

GFC, (202:w = 0, CI = 1.000; 203:w = 512, CI = 0.230; 204:w = 512, CI = 0.156; 205:w = 512, CI = 0.364).

135. (NEXUS 206) olfactory foramina, presence of small foramina lateral to opening: (0) absent; (1) present. FB, (w = 1365, CI = 0.364).
136. (NEXUS 207-208) ventral margin of olfactory foramen: (0) no shelf (vertical or horizontal present); (1) horizontal shelf projecting anteriorly, but less than anterodorsal margin of frontal; (2) horizontal shelf projecting anteriorly, further anteriorly than anterodorsal margin of frontal. GFC, (207:w = 910, CI = 0.414; 208:w = 910, CI = 0.115).
137. (NEXUS 209) distinct vomerine process of the frontal (not extension of ventral margin, nor part of articulation with basisphenoid), below the olfactory foramen: (0) absent; (1) present. FB, (w = 1365, CI = 0.130).
138. (NEXUS 210-211) position of vomerine process of the frontal: (0), medial to foramen; (1) processes present both medially and laterally; (2) lateral to foramen. GFC, (210:w = 745, CI = 0.273; 211:w = 745, CI = 0.476).
139. (NEXUS 212-213) anterodorsal prefrontal process: (0) distinct from and extending anteriorly over anteroventral process; (1) distinct from, but not extending anteriorly over, anteroventral process (fused but still distinguishable]; (2) fused with anteroventral process, indistinguishable as separate processes. GFC, (212:w = 683, CI = 0.133; 213:w = 683, CI = 0.324).
140. (NEXUS 214) anteroventral prefrontal process, anteriormost point: (0) median or equal to anteriormost point of anterodorsal process; (1) lateral to anteriormost point of anterodorsal process. FB, (w = 1365, CI = 0.195).
141. (NEXUS 215) ventrolateral prefrontal process: (0) no pointed or distinct process, not triangular shaped or knobbed; (1) triangularly shaped process or rounded knob present. FB, (w = 1365, CI = 1.000).
142. (NEXUS 216) ventrolateral prefrontal process: (0) does not extend further ventrally than floor of olfactory foramen; (1) does extend further ventrally than floor of olfactory foramen. FB, (w = 1365, CI = 0.174).
143. (NEXUS 217) ventrolateral prefrontal process: (0) does not connect directly to anteroventral process, large concavity separates two processes; (1) connects directly to anteroventral process, forming single cotyle within margins. FB, (w = 1365, CI = 0.828).
144. (NEXUS 218-219) ventral surface, small sagittal and vertical ridge or lip which outlines articulation of dorsal plate of basisphenoid: (0) absent; (1) present, though maybe not present for entire length of ventral surface; (2) present for entire length of ventral surface. GFC, (218:w = 683, CI = 0.214; 219:w = 683, CI = 0.212).
145. (NEXUS 220) oblique groove in ventral surface, just posterior to olfactory foramen, running posterolaterally from anteromedial corner: (0) absent; (1) present. FB, (w = 1365, CI = 0.615).
146. (NEXUS 221) tongue-in-groove caudoventral process for basisphenoid articulation: (0) present, but does not extend posteriorly from rest of bone, reduced; (1) present,

extending posteriorly from rest of bone as flat, wide process. FB, (w = 1365, CI = 0.375).

147. (NEXUS 222) articulated specimens: minimum width across both frontals: (0) less than or equal to width of skull at anterior end of supratemporals; (1) greater than width of skull at anterior end of supratemporals [modified from Gutberlet, 1998a]. FB, (w = 1365, CI = 0.231).

PARIETAL

148. (NEXUS 223) parietal: (0) as wide as long; (1) longer than wide - measured at widest points (include postfrontal processes, not postfrontals). FB, (w = 1365, CI = 0.143).
149. (NEXUS 224) postorbital process: (0) without distinct channel/groove for postfrontal; (1) with deep channel/groove. FB, (w = 1365, CI = 0.113).
150. (NEXUS 225) channel for secondary anterior opening of the vidian canal: (0) absent or weakly developed, present only as slight groove or indentation; (1) strongly developed, with lateral walls forming channel (~ 50% of foramen margin formed by parietal). FB, (w = 1365, CI = 0.233).
151. (NEXUS 226) ventrolateral wall of parietal, in region of telencephalon 'bulge': (0) moderately convex; (1) greatly convex. - region of attachment for retractor palatini and levator pterygoidei. FB, (w = 1365, CI = 0.141).
152. (NEXUS 227) presence of 'secondary' horizontal ridge on lateral parietal wall, ventral to lateral process: (0) absent; (1) present. FB, (w = 1365, CI = 0.138).
153. (NEXUS 228) position of 'secondary' horizontal ridge on lateral parietal wall: (0) present across dorsolateral face of parietal; (1) present across lateroventral face of parietal. Not polymorphic, (w = 32767, CI= 0.500).
154. (NEXUS 229) thickness of dorsolateral horizontal ridge on lateral parietal wall: (0) thickness weak, no large recess formed between secondary ridge and lateral process; (1) thickness large, creates concavity between secondary ridge and dorsolateral process. FB, (w = 1365, CI = 0.192).
155. (NEXUS 230-232) size of lateral process not dorsal to prootic: (0) absent or only small ridge of bone - does not form a shelf; (1) small - not attached to postfrontal process; (2) small, but attached to postfrontal process; (3) large - attached to postfrontal process. GFC, (230:w = 455, CI = 0.158; 231:w = 455, CI = 0.155; 232:w = 455, CI = 0.186).
156. (NEXUS 233) vertical/oblique thin lateral shelf, forming posterior margin with prootic: (0) absent; (1) present. FB, (w = 1365, CI = 0.270).

POSTFRONTAL

157. (NEXUS 234-236) postfrontal and parietal (articulated specimens): what percentage of the postorbital process (comprised by the parietal and/or the postfrontal) is bordered by the parietal: (0) none [postfrontal contacts frontal]; (1) between none and

one-third the distance; (2) between one-third and two-thirds the distance; (3) more than two-thirds the distance. GFC, (234:w = 455, CI = 0.200; 235:w = 455, CI = 0.120; 236:w = 455, CI = 0.600).

PROOTIC

158. (NEXUS 237-238) trigeminal foramen: (0) not separated by a bony partition (laterosphenoid in part); (1) separated by incomplete bony partition; (2) separated by complete bony partition [modified from Gutberlet, 1998a]. GFC, (237:w = 0, CI = 1.000; 238:w = 1365, CI = 0.245).
159. (NEXUS 239-240) foramen for re-entry of CID nerve, lateral opening: (0) margin shared with parietal; (1) greater than 90% margin within prootic, almost completely enclosed; (2) entirely within prootic. GFC, (239:w = 745, CI = 0.250; 240:w = 745, CI = 0.417).
160. (NEXUS 241-242) placement of foramen for posterior branch of pterygoid division of trigeminal (V_4) in ventrolateral surface of prootic: (0) separate foramen absent; (1) present, but as incomplete foramen on posterior margin of laterosphenoid [modified from Gutberlet, 1998a] present, (2) present as separate foramen. GFC, (241:w = 683, CI = 0.134; 242:w = 683, CI = 0.154).
161. (NEXUS 243) auditory foramen: (0) not complete, otooccipital forms posterior margin; (1) contained entirely within prootic. FB, (w = 1365, CI = 0.264).
162. (NEXUS 244) interior foramen anterior of auditory foramen: (0) complete, entire; (1) incomplete, confluent with incomplete auditory foramen - reduction in bone. FB, (w = 1365, CI = 0.828).
163. (NEXUS 245) anteroposterolateral corner: (0) sharp 90 degree drop to lateral face from horizontal dorsal prootic roof; (1) no sharp 90 degree drop to lateral face from horizontal dorsal prootic roof. FB, (w = 1365, CI = 0.195).
164. (NEXUS 246-247) anteroposteolateral edge: (0) not concave; (1) moderately concave, depth than 1/2 width of V3 foramen; (2) strong concave, depth greater than 1/2 width of V3 foramen. GFC, (246:w = 0, CI = 1.000; 247:w = 1638, CI = 0.253).

OTOOCCIPITAL

165. (NEXUS 248) size of medial aperture of recessus scalae tympani: (0) lesser than or equal to medial aperature of vagus nerve; (1) greater than medial aperature of vagus nerve. FB, (w = 1365, CI = 0.157).
166. (NEXUS 249) medial foramen for glossopharyngeal nerve (IX): (0) separate foramen absent; (1) separate foramen on medial surface of otooccipital. FB, (w = 1365, CI = 0.200).
167. (NEXUS 250) margin of horizontal semicircular canal, medial to posterior ampullary recess for ampulae of posterior SSC: (0) mostly entire (bony) or continuous to articulation with supraoccipital; (1) substantial portion of anterolateral margin absent, not continuous with supraoccipital. FB, (w = 1365, CI = 0.246).

168. (NEXUS 251) entire small foramen between perilymphatic and posterior ampullary recess for ampulae of posterior SSC, or in margin of either one of aforementioned foramina: (0) absent; (1) present. FB, (w = 1365, CI = 0.261).
169. (NEXUS 252-255) number of medial (hypoglossal?) nerve foramina, posterodorsal to process above. GFC, (252:w = 520, CI = 0.500; 253:w = 520, CI = 0.169; 254:w = 520, CI = 0.270; 255:w = 0, CI = 1.000).
170. (NEXUS 256-259) number of lateral (hypoglossal?) nerve foramina, posterior to jugular foramen recess (not including nerve foramina on dorsal roof). GFC, (256:w = 520, CI = 0.583; 257:w = 520, CI = 0.150; 258:w = 520, CI = 0.214; 259:w = 0, CI = 1.000).
171. (NEXUS 260-261) lateral jugular foramen, presence of additional foramina deep within same lateral depression - not including variable placement of lateral glossopharyngeal foramen: (0) no other foramen present; (1) one additional foramen present; (2) two or more additional foramina present. GFC, (260:w = 910, CI = 0.231; 261:w = 910, CI = 0.145).
172. (NEXUS 262) dorsal surface, near articulation with prootic: (0) rounded surface, no vertically or coronally oriented shelf at transition between "lower otooccipital roof" and "upper prootic roof"; (1) vertical or coronally oriented shelf, or sharp ~90 degree angle (or crest), at transition between "two" roofs. FB, (w = 1365, CI = 0.500).
173. (NEXUS 263) extension of dorsal margin of crista circumfenestralis: (0) not past posterior roof margin (forming dorsal margin of foramen magnum); (1) past posterior roof margin (forming dorsal margin of foramen magnum). FB, (w = 1365, CI = 0.278).
174. (NEXUS 264) extension of dorsal margin of crista circumfenestralis: (0) narrow peg-like or narrow crescent-shaped extension; (1) or not peg-like or narrow crescent-shaped extension. FB, (w = 1365, CI = 0.526).
175. (NEXUS 265) posterior dorsal margin and dorsal margin of crista circumfenestralis continuous forming horizontal shelf: (0) absent; (1) present. FB, (w = 1365, CI = 0.164).
176. (NEXUS 266) juxtapedial recess, size: (0) longer than tall; (1) not longer than tall. narrowest distances measured between lateral crista circumfenestralis border and margin of fenestra ovalis; also widest distance between inner margins of dorsal and ventral articulations with prootic. FB, (w = 1365, CI = 0.157).

SUPRAOCCIPITAL

177. (NEXUS 267-268) midsagittal crest: (0) defined crest absent; (1) not present to tip of posterior process; (2) present to tip of posterior process. GFC, (267:w = 910, CI = 0.150; 268:w = 910, CI = 0.176).
178. (NEXUS 269-270) "parasagittal crests": (0) present only as rounded edges, elevated over semicircular canal, nothing distinct; (1) not distinct entire length, rounded and flattened towards posterior margin; (2) distinct entire length, not rounded or flattened towards posterior margin. GFC, (269:w = 910, CI = 0.174; 270:w = 910, CI = 0.195).

179. (NEXUS 271) posterior margin: (0) no well-defined point or process at posteriormost region, more rounded than pointed; (1) well-defined point or process at posteriormost region, distinct process. FB, (w = 1365, CI = 0.333).
180. (NEXUS 272) width of dorsal roof along midline (same height as dorsal surface of parietal): (0) less than 1/2 length of dorsal roof at widest length; (1) greater than 1/2 length of dorsal roof at widest length. FB, (w = 1365, CI = 0.375).
181. (NEXUS 273-276) roof measurement: length midline length/width at widest point – length/width ratio divided into bins 0.1 (0.4 – 0.8). GFC, (273:w = 496, CI = 0.333; 274:w = 496, CI = 0.189; 275:w = 496, CI = 0.192; 276:w = 496, CI = 1.000).

BASIOCCIPITAL

182. (NEXUS 277) anterior margin, shared with basisphenoid: (0) entire; (1) notched at midline. FB, (w = 1365, CI = 0.203).
183. (NEXUS 278) ventral process, distal end: (0) single; (1) bifurcate [modified from Gutberlet, 1998a]. FB, (w = 1365, CI = 0.146).
184. (NEXUS 279) ventral process: (0) single solid and fused element; (1) two or more distinct elements together comprising process, visible along anterior midline. FB, (w = 1365, CI = 0.198).
185. (NEXUS 280) ventral process: (0) thin, flat with no anterior lateral struts; (1) thick, with anterior lateral struts. FB, (w = 1365, CI = 0.333).
186. (NEXUS 281) ventral process, recurved such that it curves back past its posterodorsal origin: (0) no; (1) yes. FB, (w = 1365, CI = 0.110).
187. (NEXUS 282) which ventral process more “ventral”: (0) about equal, but basioccipital (1) basioccipital (not close). FB, (w = 1365, CI = 0.375).
188. (NEXUS 283-284) ventral surface, presence of foramen between ventral and condylar processes: (0) absent; (1) single foramen present; (2) more than one present. GFC, (283:w = 683, CI = 0.161; 284:w = 683, CI = 0.128).
189. (NEXUS 285) ventral surface, concavity between ventral and condylar processes: (0) absent; (1) present. FB, (w = 1365, CI = 0.115).
190. (NEXUS 286) height vs. length (midline): (0) longer than tall; (1) taller than long. FB, (w = 1365, CI = 0.714).

SPHENOID

191. (NEXUS 287-288) height of ventral process: (0) absent, only elevated or rounded edge or nothing; (1) low vertical edge; (2) conspicuous high vertical edge. GFC, (287:w = 745, CI = 0.235; 288:w = 745, CI = 0.124).
192. (NEXUS 289) elevated ventral process continuous to posterior edge: (0) no; (1) yes. FB, (w = 1365, CI = 0.286).
193. (NEXUS 290-291) ventral process continuous to anterior edge as vertical (albeit short) shelf of bone, not as rounded ridge: (0) absent; (1) present, but terminates inside (against) anterior margin of concavity); (2) present and entire. GFC, (290:w = 683, CI = 0.127; 291:w = 683, CI = 0.250).

194. (NEXUS 292) ventral process, highest peak: (0) anterior or (1) posterior portion of basisphenoid region of sphenoid. FB, (w = 1365, CI = 0.220).
195. (NEXUS 293) ventral process, number of peaks: (0) only single peak, (1) more than one. FB, (w = 1365, CI = 0.112).
196. (NEXUS 294) distal point on ventral process: (0) not divided; (1) divided. FB, (w = 1365, CI = 0.190).
197. (NEXUS 295) small ventrolateral process of basisphenoid region (majority ventral to horizontal shelf), posterior to secondary anterior vidian opening: (0) absent; (1) present. FB, (w = 1365, CI = 0.224).
198. (NEXUS 296) pituitary recess, carotid canals and foramina in lateral margins: (0) diameter of right side reduced, ~ half diameter of left; (1) diameter of both left and right sides roughly equivalent. FB, (w = 1365, CI = 0.154).
199. (NEXUS 297) foramen for entrance of abducens nerve (VI), posterior to dorsum sella: (0) absent; (1) present. FB, (w = 1365, CI = 1.000).
200. (NEXUS 298) common foramen on posteroventral surface with entrance of both vidian canal and cerebral branch of internal carotid artery: (0) no common foramen; (1) common foramen. Not polymorphic, (w = 32767, CI = 1.000).
201. (NEXUS 299-300) secondary roof formed in anterior portion of vidian canal, forming secondary foramina (either side): (0) no - completely open; (1) yes (at least one side); (2) no - completely roofed. GFC, (299:w = 1820, CI = 0.250; 300:w = 1820, CI = 0.600).
202. (NEXUS 301) horizontal ridge between anteriormost lateral processes that articulate with parietal: (0) absent; (1) present, well defined. FB, (w = 1365, CI = 0.600).
203. (NEXUS 302) frontal step of cultiform process: (0) absent; (1) present. FB, (w = 1365, CI = 0.692).
204. (NEXUS 303-304) frontal step of cultiform process; (0) only present laterally (two separate steps separated by continuous cultiform) or present and not complete; (1) present (and entire); (2) only present medially. GFC, (303:w = 683, CI = 0.462; 304:w = 683, CI = 0.286).
205. (NEXUS 305) cultiform process, anterior edge: 0) dorsal and ventral surface separate; (1) dorsal and ventral surface fused. FB, (w = 1365, CI = 0.667).
206. (NEXUS 306-308) cultiform process, anterior edge: (0) ventral surface extends farther anterior than dorsal surface; (1) dorsal and ventral surface extend roughly equal distance anteriorly; (2) dorsal surface extends slightly farther anterior, less than 2x width of anterior vidian canal; (3) dorsal surface extends conspicuously more anterior than ventral process, greater than 2x width of anterior vidian canal. GFC, (306:w = 455, CI = 0.253; 307:w = 455, CI = 0.131; 308:w = 455, CI = 0.545).
207. (NEXUS 309) width of pterygoid process (0) does not extend or (1) does extend beyond width of basisphenoid region. FB, (w = 1365, CI = 0.110).

ADDITIONAL CHARACTERS

208. (NEXUS 310) rattle: (0) absent; (1) present. Not polymorphic, (w = 32767, CI = 1.000).

209. (NEXUS 311) head plates: (0) nine large head plates; (1) more than nine head plates, broken into smaller scales. Not polymorphic, (w = 32767, CI = 0.333).

ND5

1 – 477. (NEXUS 312-788)

12S/ $tRNA^{Val}$ /16S

1 – 1905. (NEXUS 789-2693): ambiguously aligned sites: NEXUS 820, 846, 1009, 1049, 1072, 1135, 1195-1197, 1207, 1219-1222, 1228-1234, 1241-1242, 1247, 1291, 1313-1314, 1346, 1376, 1395, 1402-1403, 1417, 1450, 1461, 1480, 1486-1488, 1700-1701, 1729-1730, 1746, 1750, 1817-1835, 1883, 1888, 1893-1895, 1981-1991, 2008, 2023, 2043, 2083-2084, 2120, 2194-2195, 2211, 2233, 2278, 2494, 2505, 2516, 2526, 2693.

Appendix E

Photographs of osteological characters

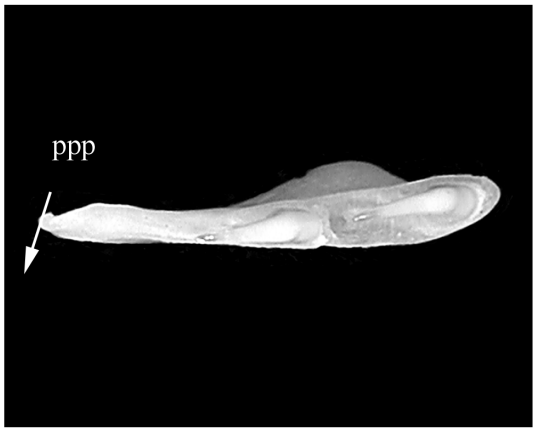
Characters 16-207 (and all associated character states) are illustrated within this appendix (save numbers of palatine, pterygoid, and dentary teeth). Underneath each figure is a brief legend. Key to legend as follows

> character number (character state): museum number, taxon ([right or left] cranial element, view [dorsal, lateral, etc.]); brief description of character state.

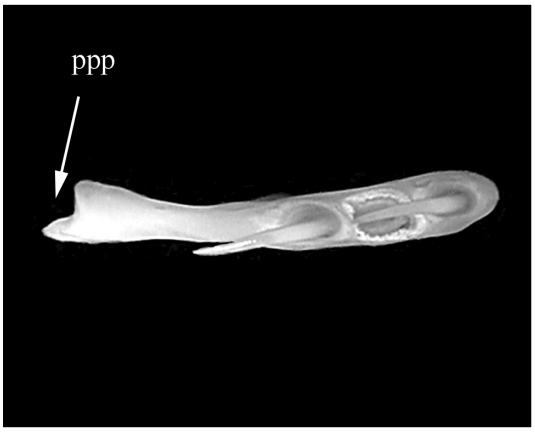
Full descriptions of each character are listed in Appendix D. Arrows are often used to indicate specific process or foramen illustrated. A list of short abbreviations for these processes/foramina are listed below:

acp - apex of choanal process (palatine)
adpp - anterodorsal prefrontal process (frontal)
af - auditory foramen (prootic)
ang - angular
app - ascending process of the premaxilla
ar - posterior ampullary recess for ampulae of posterior semi-circular canal (otoccipital)
art - articular
avpp - anteroventral prefrontal process (frontal)
awp - anteromedial wall process (maxilla)
cid - foramen for re-entry of the CID nerve (prootic)
cp - choanal process (palatine)
dalp - dorsal anterolateral process (prefrontal)
dap - dorsal articular process (maxilla)
dent - dentary
dlp - dorsolateral process (septomaxilla)
dmcc - dorsal margin of crista circumfenestralis (otoccipital)
dplp - dorsal posterolateral process (prefrontal)
dpp - dorsal prefrontal process (maxilla)
dpps - dorsoposterior process (septomaxilla)
ec - ectopterygoid
gf - glossopharyngeal nerve (otoccipital)
in - intercalary nodule
jr - juxtapedial recess (otoccipital)
lfdap - lateral fork, dorsal articular process (maxilla)
ljf - lateral jugal foramen (otoccipital)

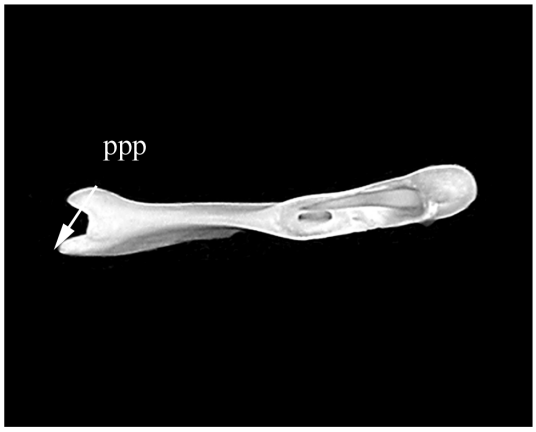
lmp - lateral maxillary process (ectopterygoid)
marst - medial aperature of recessus scalae tympani (otoccipital)
max - maxilla
mfdap - medial fork, dorsal articular process (maxilla)
mmp - medial maxillary process (ectopterygoid)
mplp - middle posterolateral process (prefrontal)
mpp - median palatal process (premaxilla)
msc - midsagittal crest (supraoccipital)
nas - nasal
olf - olfactory foramen (frontal)
oto - otoccipital
pal - palatine
par - parietal
pf - postfrontal
plf - perilymphatic foramen (otoccipital)
pmax - premaxilla
pn - processus nasalis (premaxilla)
pp - pterygoid process (sphenoid)
ppp - posterior pterygoid process (palatine)
prm - posterior dorsal margin (otoccipital)
psc - parasagittal crests (supraoccipital)
pt - pterygoid
pvl - posterior vertical lamina (vomer)
quad - quadrate
sep - septomaxilla
so - supraoccipital
sovc - secondary opening of vidian canal (parietal)
spl - splenial
st - supratemporal
V3 – mandibular branch of trigeminal nerve (V_3) foramen (prootic)
vap - ventral articular process (maxilla)
vf - vagus foramen (otoccipital)
vmop - ventral margin olfactory foramen (frontal)
vo - vomer
vlpp - ventrolateral prefrontal process (frontal)
vplp - ventral posterolateral process (prefrontal)
vvl - ventral vertical lamina (vomer)



17(0): CJB 1062, *pricei* (rt. palatine, ventral); posterior pterygoid process not forked or saddled.



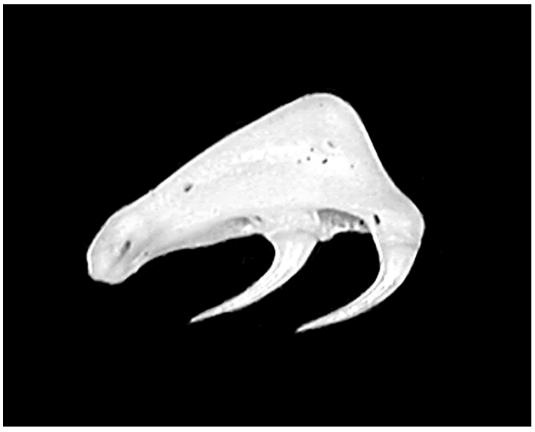
17(1): CJB 577, *atrox* (rt. palatine, ventral); posterior pterygoid process cupped or saddled.



17(2): CJB 001, *atrox* (rt. palatine,ventral); posterior pterygoid process forked or grooved.

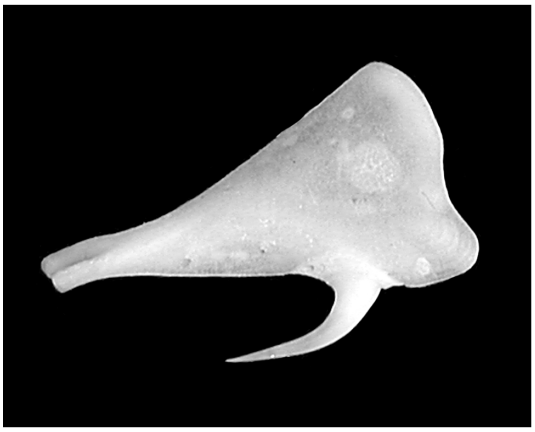
18(0): CJB 001, *atrox* (rt. palatine, lateral); ventral margin approx. equal to dorsal height.

18(1): CJB 1062, *pricei* (rt. palatine, lateral); ventral margin greater than 2x dorsal height.

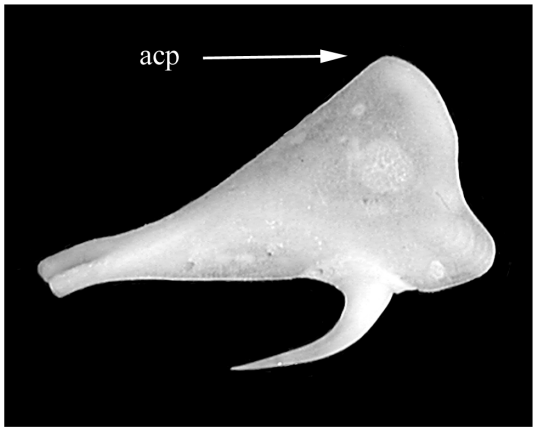


19(0): CJB 699, *cerastes* (rt. palatine, lateral); 1st tooth at anteriormost pt. along leading edge.

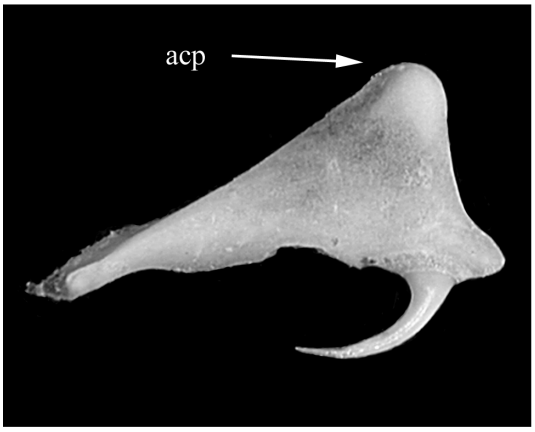
19(1): CJB 577, *atrox* (rt. palatine, lateral); 1st tooth less than tooth width posterior to leading edge.



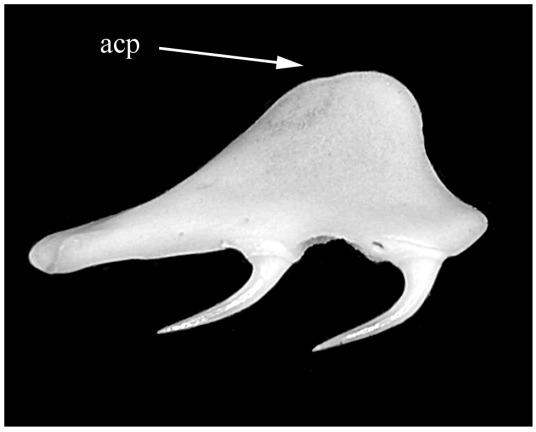
19(2): CJB 697, *molossus* (rt. palatine, lateral); 1st tooth greater than tooth width posterior to leading edge.



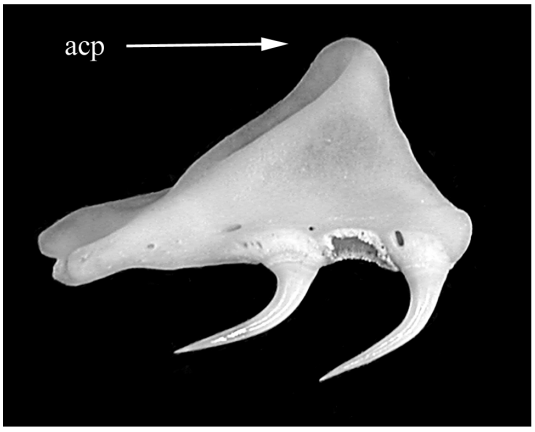
20(0): CJB 697, *molossus* (rt. palatine, lateral); apex of choanal process dorsal to position anterior to 1st tooth socket.



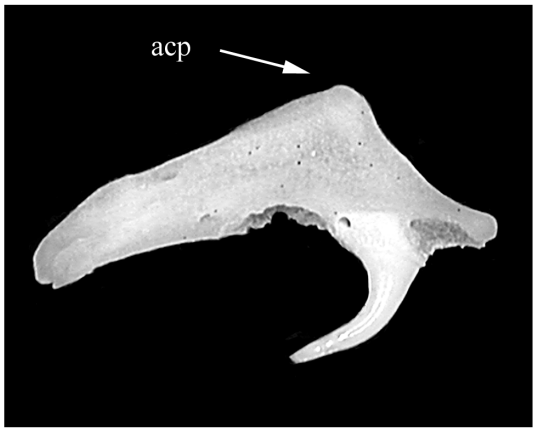
20(1): NAUQSP 14129, *molossus* (rt. palatine, lateral); apex of choanal process dorsal to 1st tooth socket.



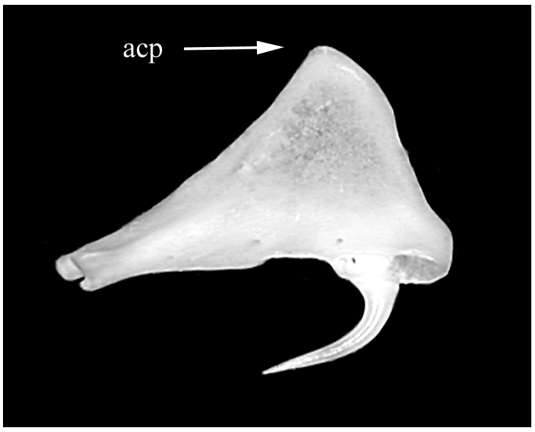
20(2): LSUMZ 10340, *horridus* (rt. palatine, lateral); apex of choanal process dorsal to position between 1st and medial socket.



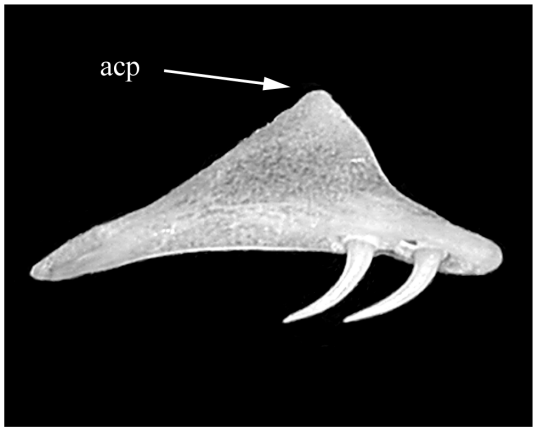
20(3): CJB 577, atrox (rt. palatine, lateral); apex of choanal process dorsal to medial socket.



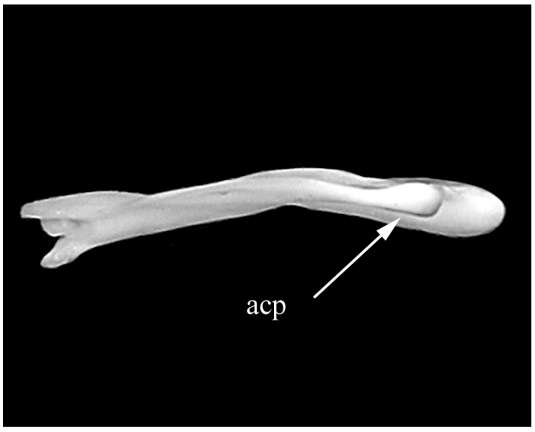
20(4): CJB 1061, *lepidus* (rt. palatine, lateral); apex of choanal process dorsal to position between medial and last socket.



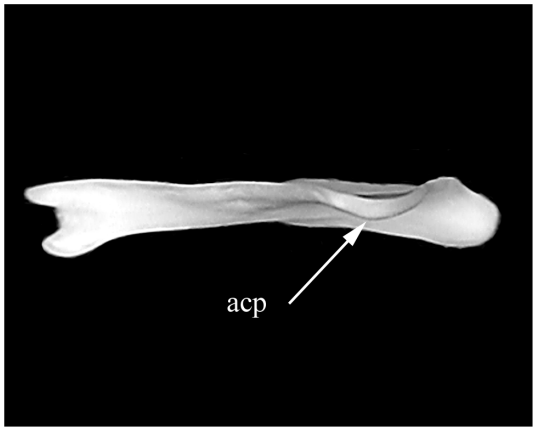
20(5): CJB 001, *atrox* (rt. palatine, lateral); apex of choanal process dorsal to last tooth socket.



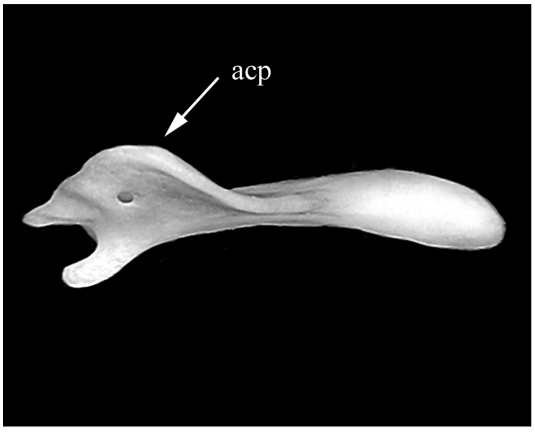
20(6): CJB 690, *miliarius* (rt. palatine, lateral); apex of choanal process dorsal and posterior to last tooth socket.



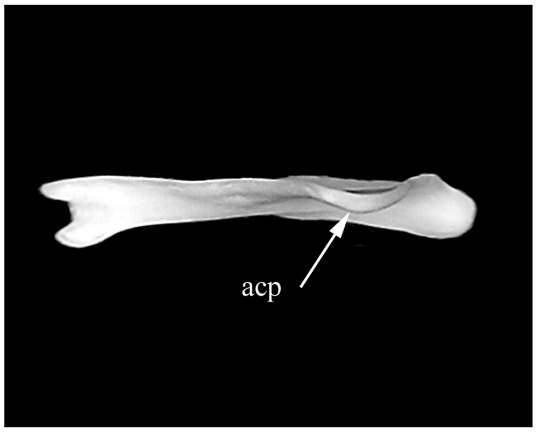
21(0): LSUMZ 29584, *adamanteus* (rt. palatine, dorsal); apex of choanal process not curved.



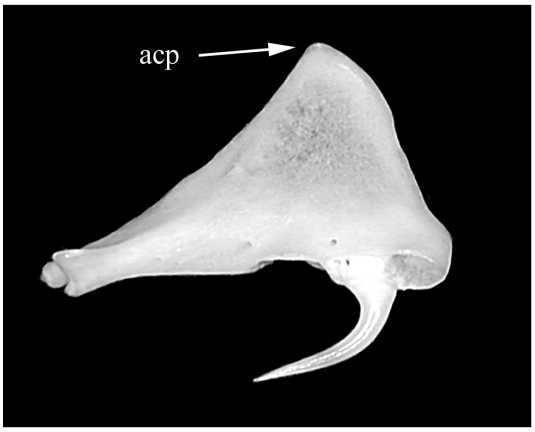
21(1): CJB 001, *atrox* (rt. palatine, dorsal); apex of choanal process curved.



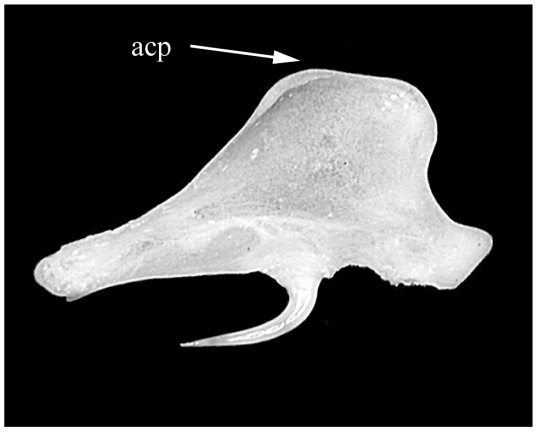
22(0): CJB 685, *piscivorus* (rt. palatine, dorsal); apex of choanal process curved medially.



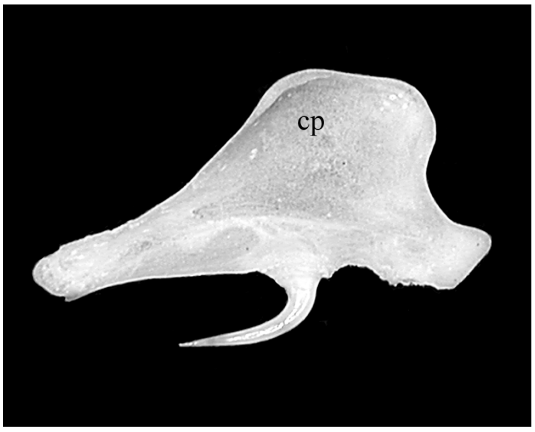
22(1): CJB 001, *atrox* (rt. palatine, dorsal); apex of choanal process curved laterally.



23(0): CJB 001, *atrox* (rt. palatine, lateral); apex of choanal process rounded.

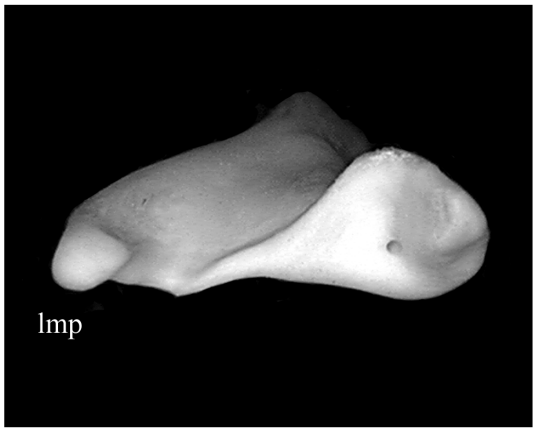


23(1): CM 145590, *horridus* (rt. palatine, lateral); apex of choanal process squared.

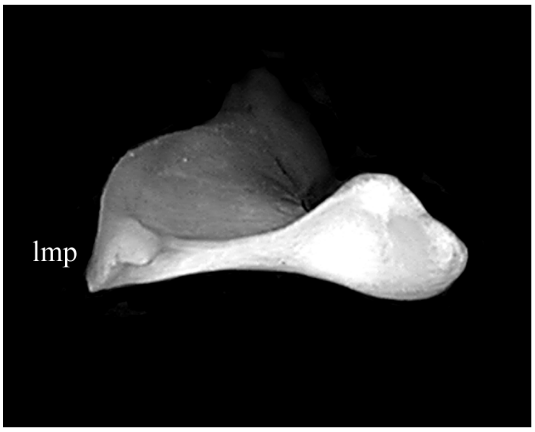


24(0): CM 145590, *horridus* (rt. palatine, lateral); posterior margin of choanal process concave.

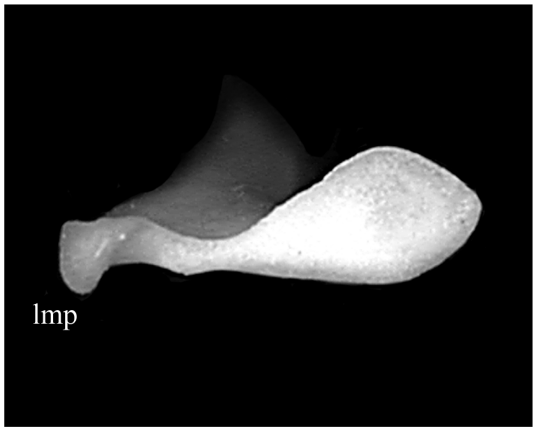
24(1); CJB 1062, pricei (rt. palatine, lateral); posterior margin of choanal process straight or convex.



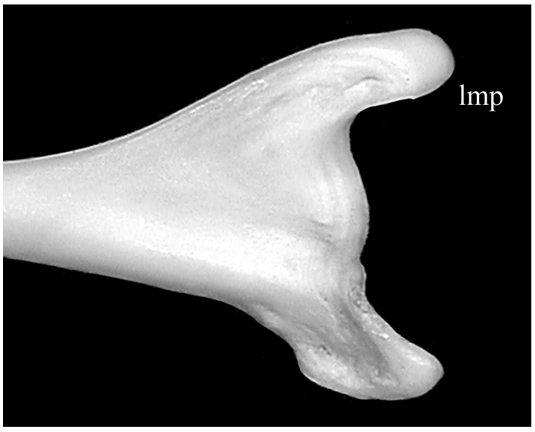
25(0): LSUMZ 29584, *adamanteus* (rt. ectopterygoid, anterior); lateral edge of lateral maxillary process w/out flat vertical face.



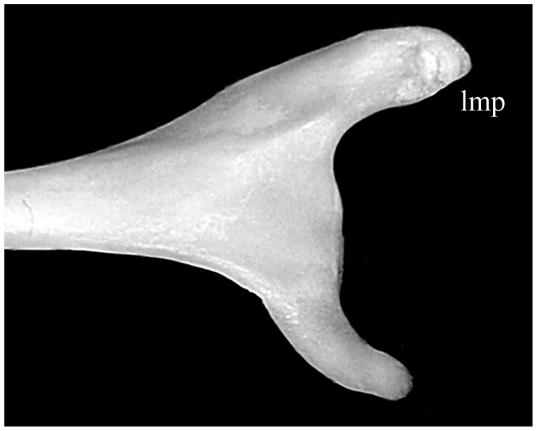
25(1): TJL 930, *polystictus* (rt. ectopterygoid, anterior); lateral edge of lateral maxillary process with flat 45 degree face.



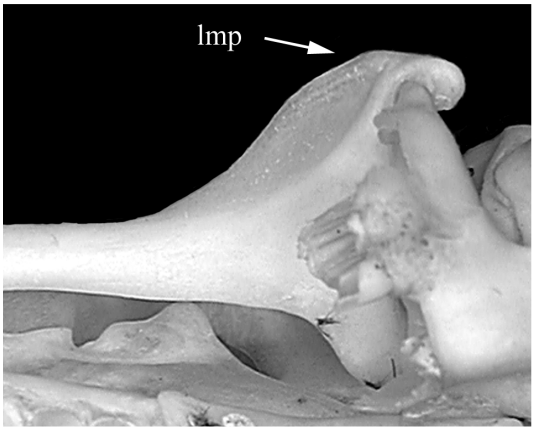
25(2): CJB 690, *miliarius* (rt. ectopterygoid, anterior); lateral edge of lateral maxillary process with flat 90 degree face.



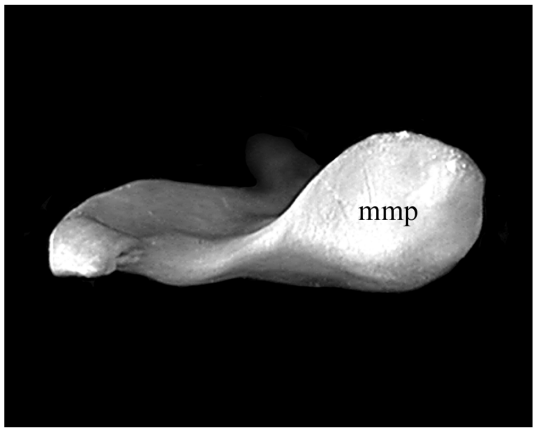
26(0): LSUMZ 29584, *adamanteus* (rt. ectopteryoid, ventral); ventrolateral surface of lateral maxillary process smooth.



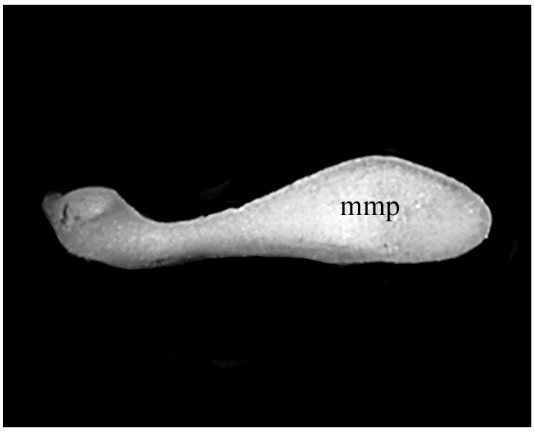
26(1): CJB 574, *atrox* (rt. ectopterygoid, ventral); ventral surface of lateral maxillary process weakly concave.



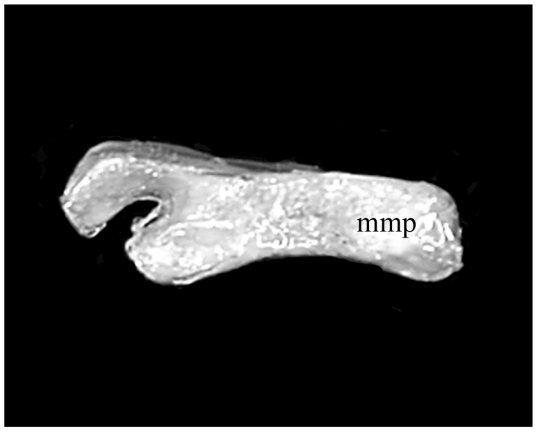
26(2): CJB 70, *durissus* (rt. ectopterygoid, ventral); ventral surface of lateral maxillary process deeply concave.



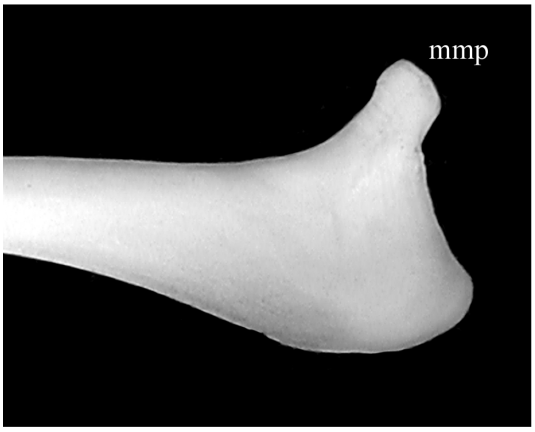
27(0): CJB 574, *atrox* (rt. ectopterygoid, anterior); medial maxillary process greater than 1/3 facet width.



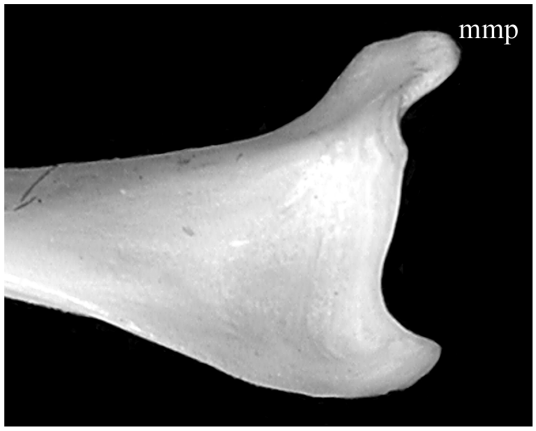
27(1): SDNHM 60383, *willardi* (rt. ectopterygoid, anterior); medial maxillary process facet height 1/3 facet width.



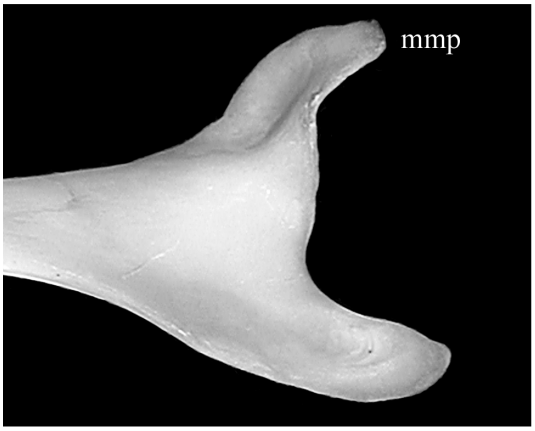
27(2): FMNH 31174, *muta* (rt. ectopterygoid, anterior); medial maxillary process facet height less than 1/3 facet width.



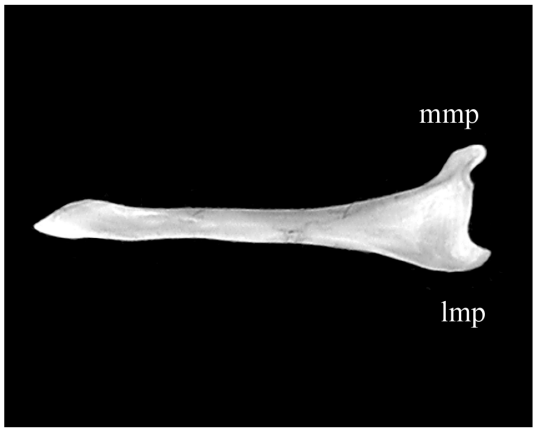
28(0): CJB 508, *piscivorus* (rt. ectopterygoid, dorsal); dorsal surface of medial maxillary process smooth or weakly convex.



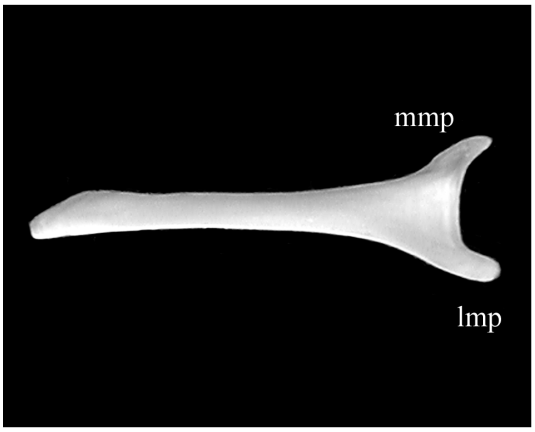
28(1): TJL 930, *polystictus* (rt. ectopterygoid, dorsal); dorsal surface of medial maxillary process weakly concave.



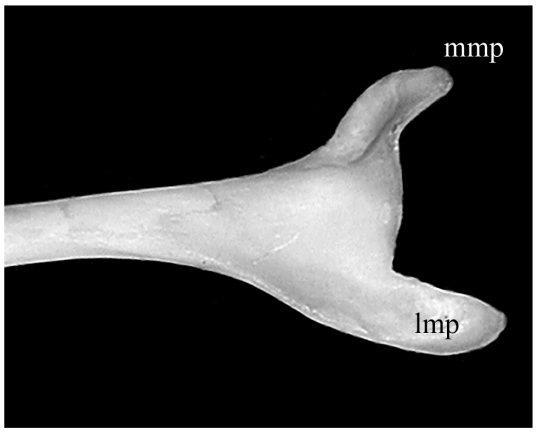
28(2): CJB 574, *atrox* (rt. ectopterygoid, dorsal); dorsal surface of medial maxillary process deeply concave.



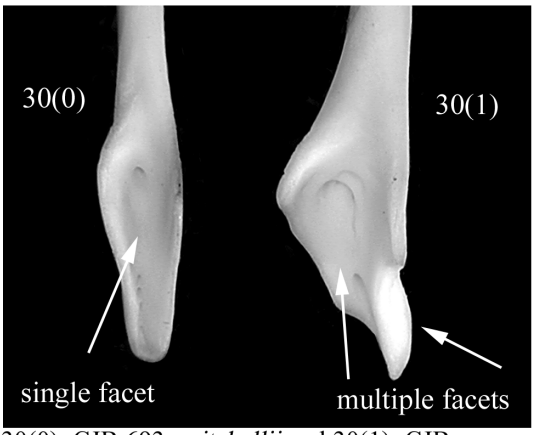
29(0): TJL 930, *polystictus* (rt. ectopterygoid, dorsal); both maxillary process extend equal distances anteriorly.



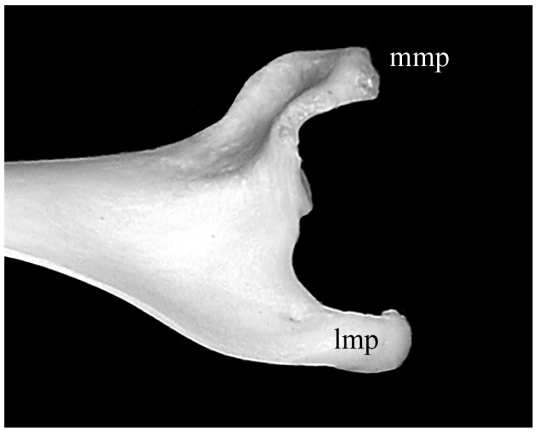
29(1): CJB 693, *mitchellii* (rt. ectopterygoid, dorsal); lateral maxillary process extends only slightly farther anteriorly.



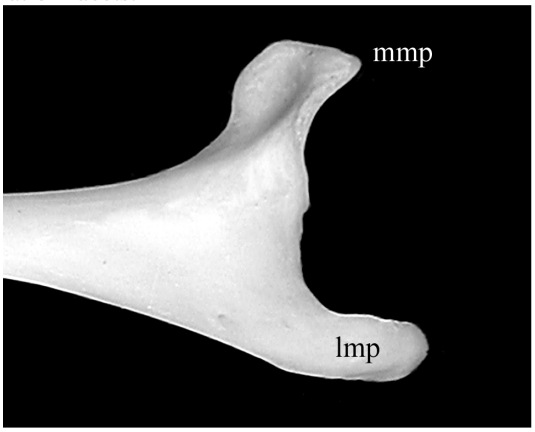
29(2): CJB 574, *atrox* (rt. ectopterygoid, dorsal); lateral maxillary process extends at least twice as far anteriorly.



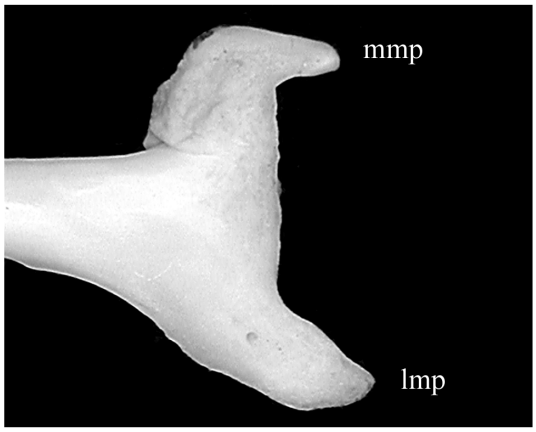
30(0): CJB 693, *mitchellii* and 30(1): CJB 508, *piscivorus* (rt. ectopterygoid, posteroventral); single vs. multiple pterygoid articulation facets.



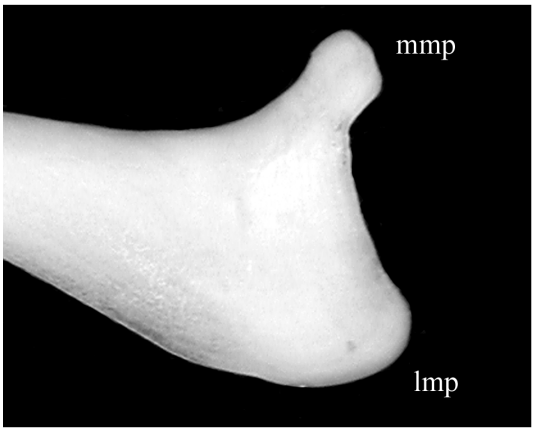
31(0): LSUMZ 34177, *adamanteus* (rt. ectopterygoid, dorsal); both maxillary processes with 90 degree interior angles.



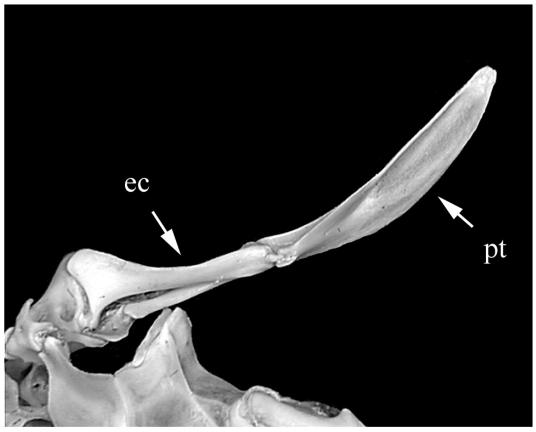
31(1): CJB 490, *ruber* (rt. ectopterygoid, dorsal); only lateral maxillary process with 90 degree interior angle.



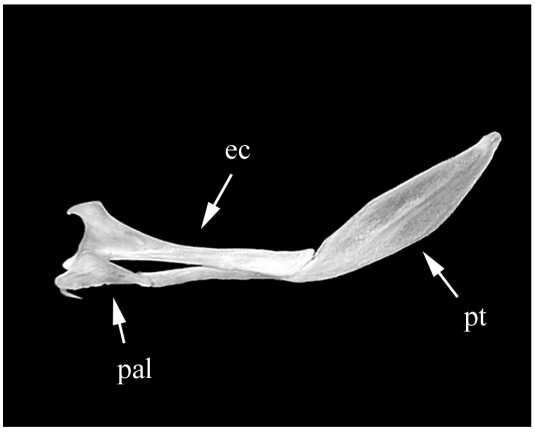
31(2): LSUMZ 29347, *durissus* (rt. ectopterygoid, dorsal); only medial maxillary process with 90 degree interior angle.



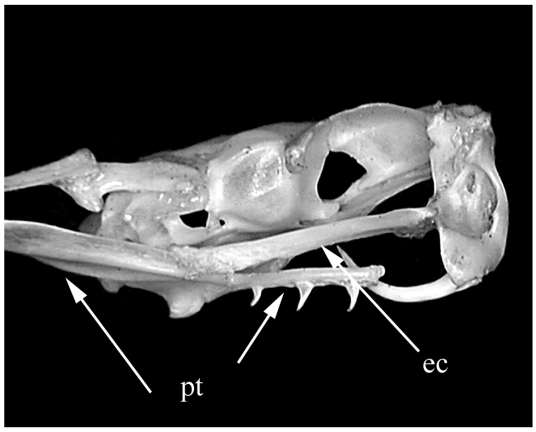
31(3): CJB 508, *piscivorus* (rt. ectopterygoid, dorsal); neither maxillary process with 90 degree interior angle.



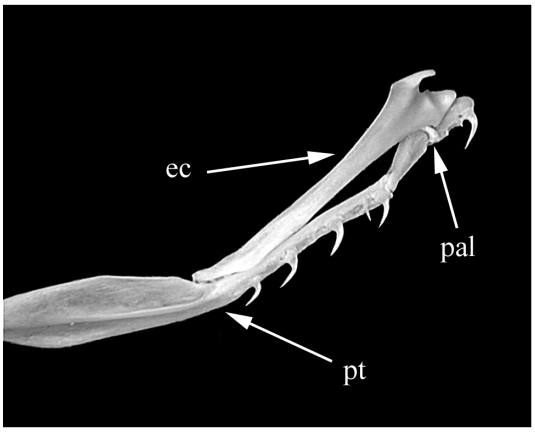
32(0): TJL 539, *piscivorus* (rt. ectopterygoid and pterygoid); ectopterygoid shorter than base of pterygoid.



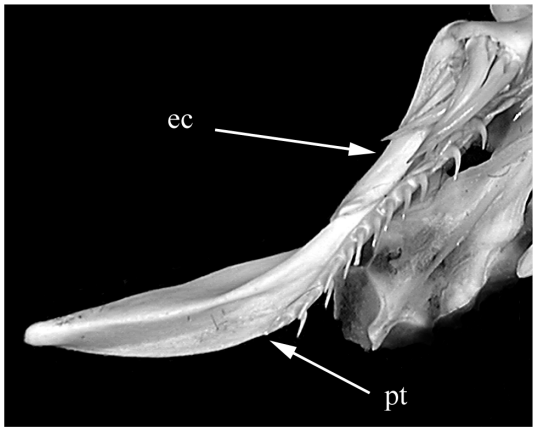
32(1): CJB 1064, *enyo* (rt. ectopterygoid and pterygoid); ectopterygoid longer than base of pterygoid.



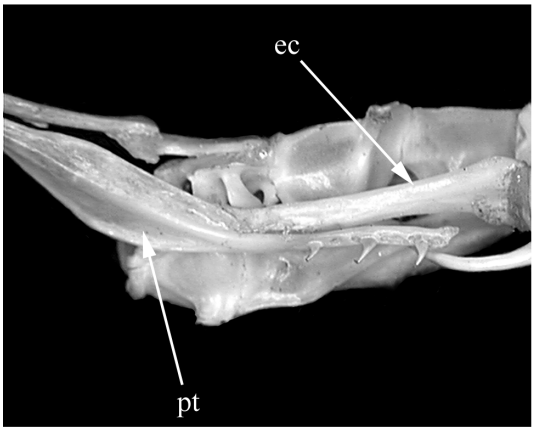
34(0): SDNHM 46986, *willardi* (rt. pterygoid); teeth only found anterior to articulation with ectopterygoid.



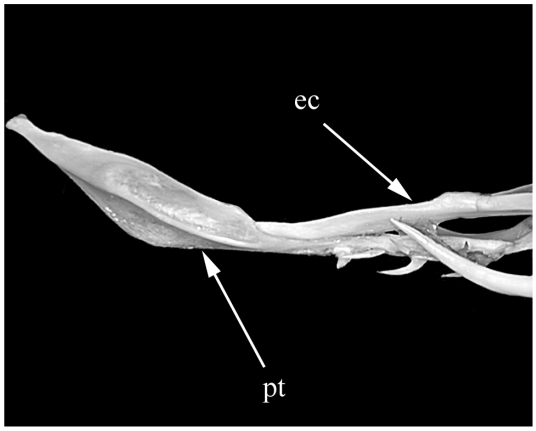
34(1): CJB 1064, *enyo* (rt. pterygoid); tooth row ends with region of articulation with ectopterygoid.



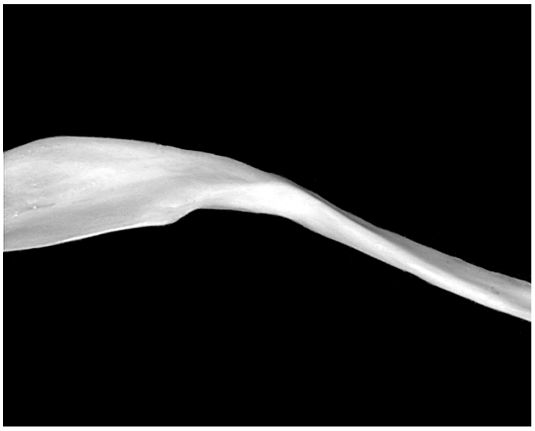
34(2): TJL 539, *piscivorus* (rt. pterygoid); tooth row ends posterior to articulation with ectopterygoid.



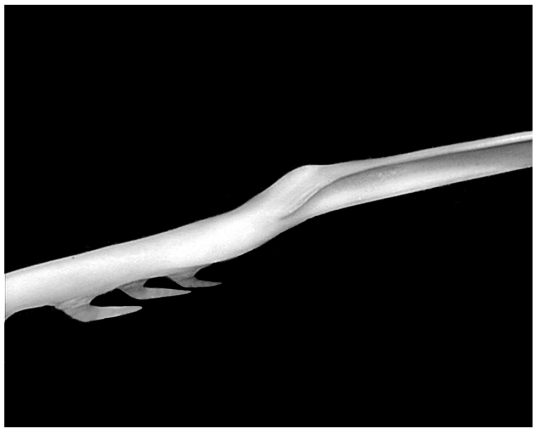
35(0): SDNHM 46986, *willardi* (rt. pterygoid); articulation of ectopterygoid within curvature of lateral pterygoid margin.



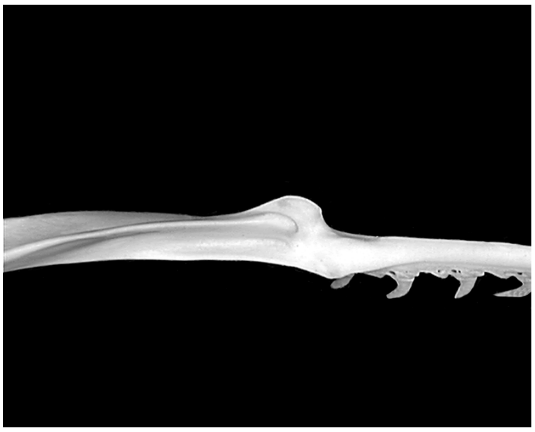
35(1): LSUMZ 55366, *polystictus* (rt. pterygoid); articulation of ectopterygoid anterior to curvature of lateral pterygoid margin.



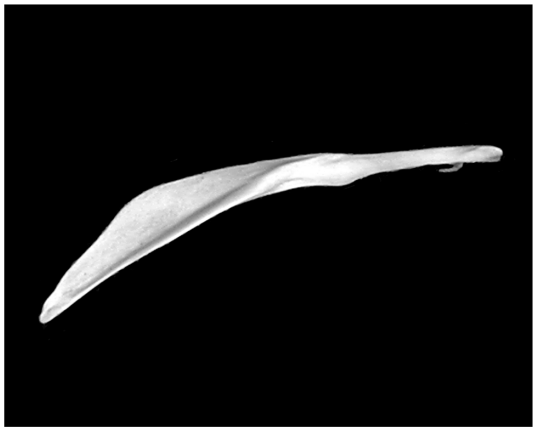
36(0): LSUMZ 29347, *durissus* (rt. pterygoid); notch absent at posteromedial edge at articulation with ectopterygoid.



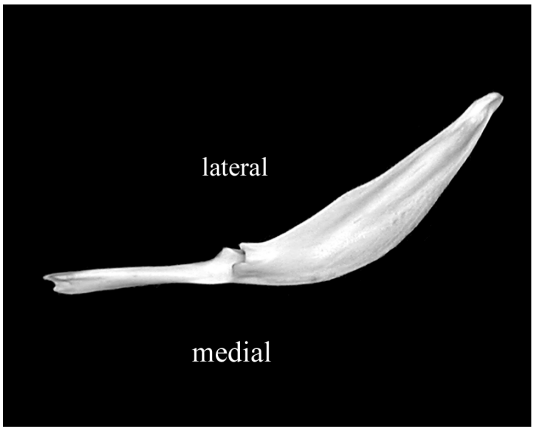
36(1): LSUMZ 29584, *adamanteus* (rt. pterygoid); notch weakly present at posteromedial edge at articulation with ectopterygoid.



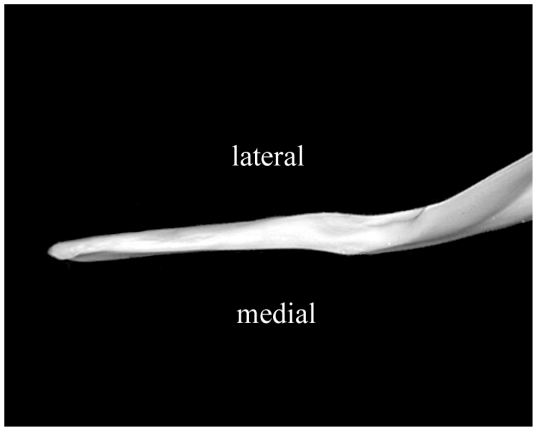
36(2): CJB 508, *piscivorus* (rt. pterygoid); notch weakly present at posteromedial edge at articulation with ectopterygoid.



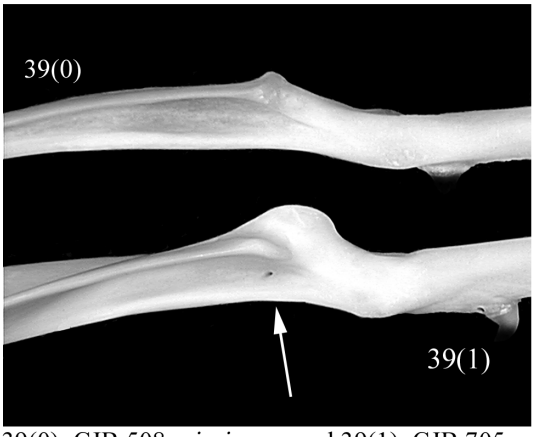
37(1): CJB 699, *cerastes* (rt. pterygoid, dorsal); dorsal concavity formed by lateral ridge.



38(0): CJB 508, *piscivorus* (rt. pterygoid, dorsal); posteriorly, lateral edge curves before medial edge.

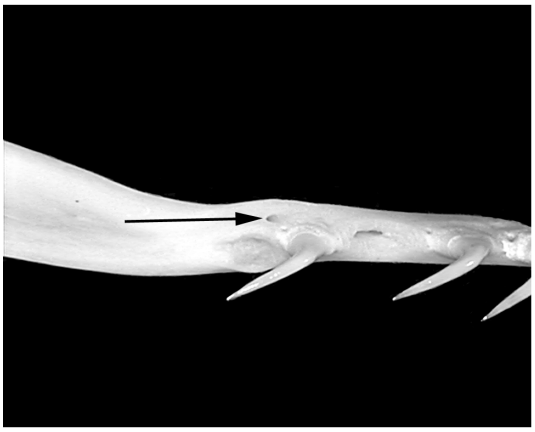


38(1): LSUMZ 29583, *atrox* (rt. pterygoid, dorsal); posteriorly, both edges curve at same point.

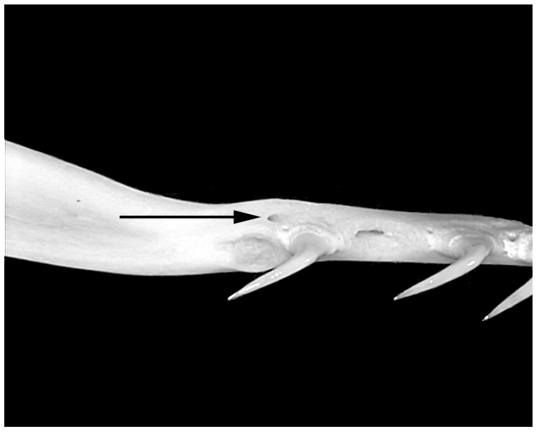


39(0): CJB 508, *piscivorus* and 39(1): CJB 705, *piscivorus* (both rt. pterygoid, ventral); foramen at anterior end of lateral ventral fossa: absent vs. present.

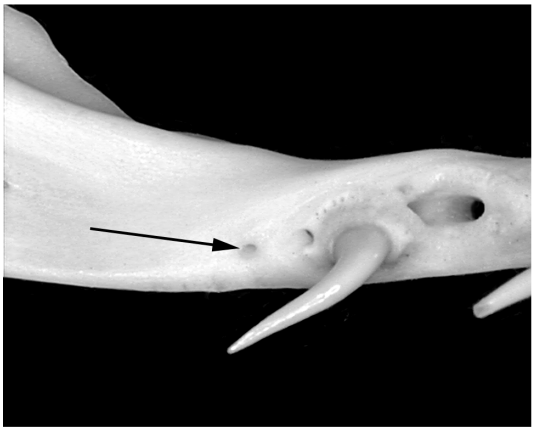
40(0): LSUMZ 29347, *durissus* (rt. pterygoid, ventral); absence of nutritive foramen at posterior end of tooth row.



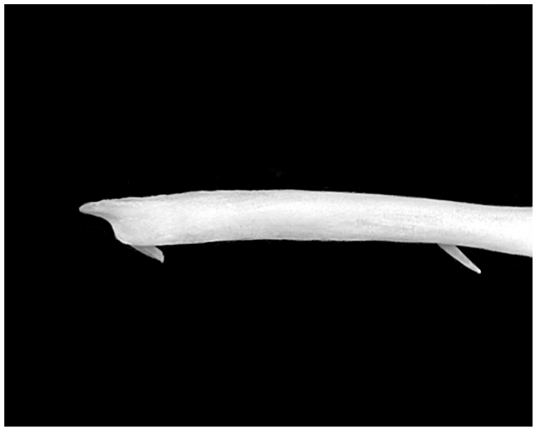
40(1): CJB 490, *ruber* (rt. pterygoid, ventral); presence of nutritive foramen at posterior end of tooth row.



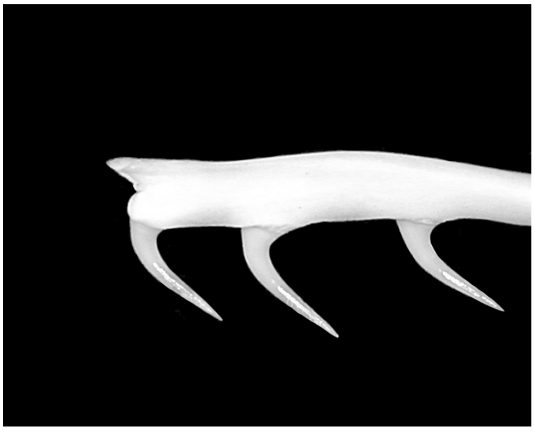
41(0): CJB 490, *ruber* (rt. pterygoid, ventral); nutritive foramen present lateral to last or penultimate tooth.



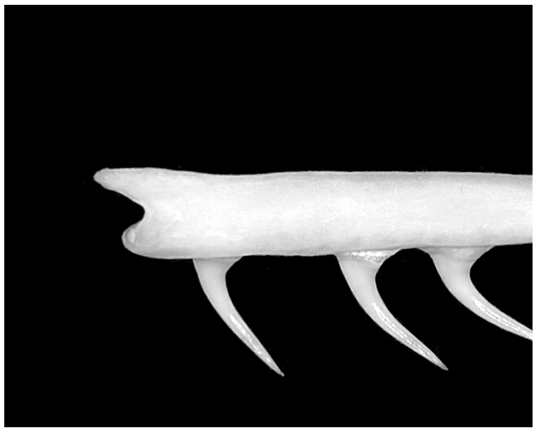
41(1): LSUMZ 34177, *adamanteus* (rt. pterygoid, ventral); nutritive foramen present posterior to last tooth.



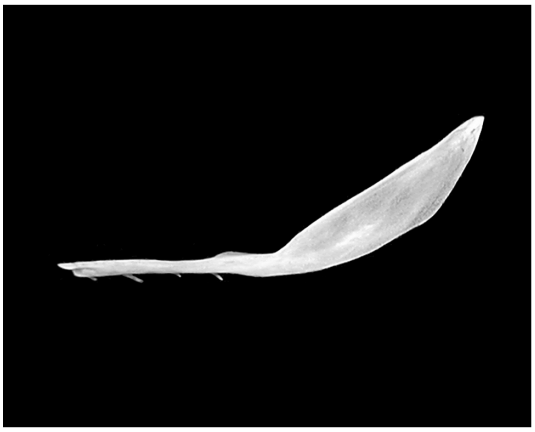
42(0): CM 145580, *cerastes* (rt. pterygoid, medial); no notch at articulation with palatine.



42(1): CJB 001, *atrox* (rt. pterygoid, medial); weakly notched at articulation with palatine.

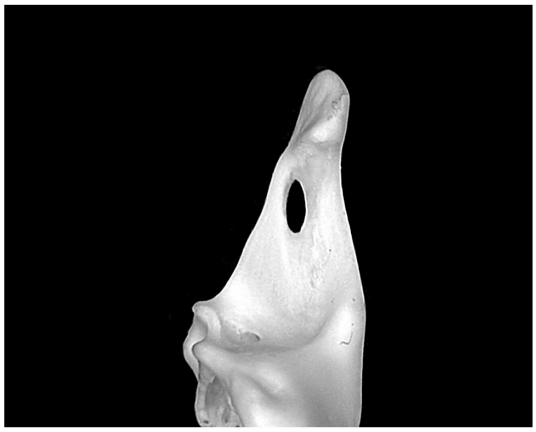


42(2): CJB 490, *ruber* (rt. pterygoid, medial); strongly notched at articulation with palatine.

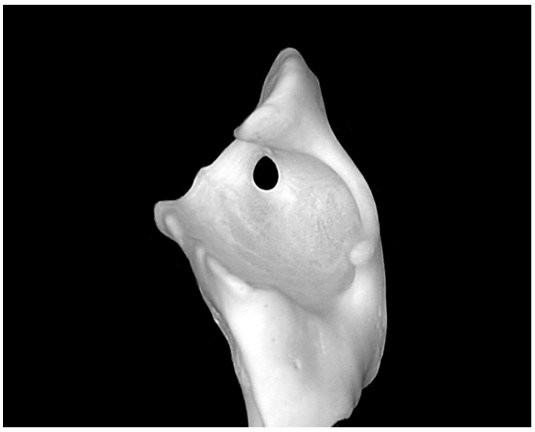


43(0): CJB 650, *cerastes* (rt. pterygoid, dorsal); straight lateral edge, no convex humps on posterior lateral edge.

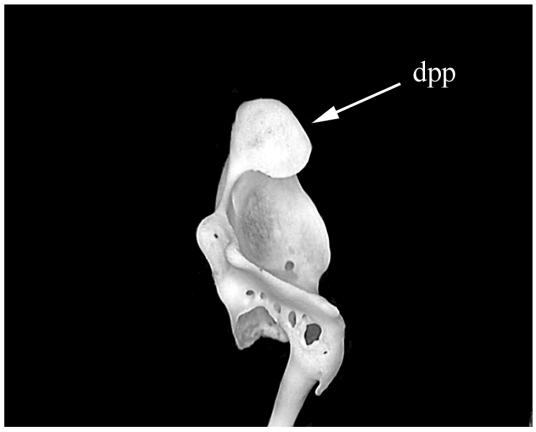
43(1): CJB 001, *atrox* (rt. pterygoid, dorsal); presence of small convex hump(s) on posterior lateral edge.



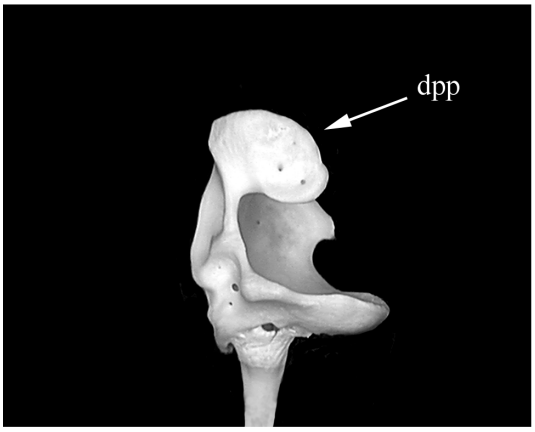
44(0): CJB 508, *piscivorus* (rt. maxilla, lateral); egg-shaped foramen.



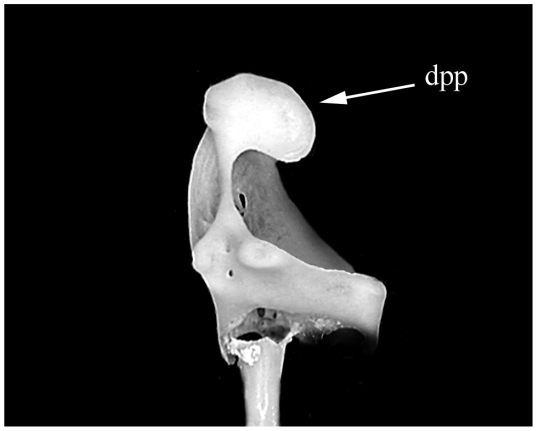
44(1): CJB 490, *ruber* (rt. maxilla, lateral); rounded, not egg-shaped, foramen.



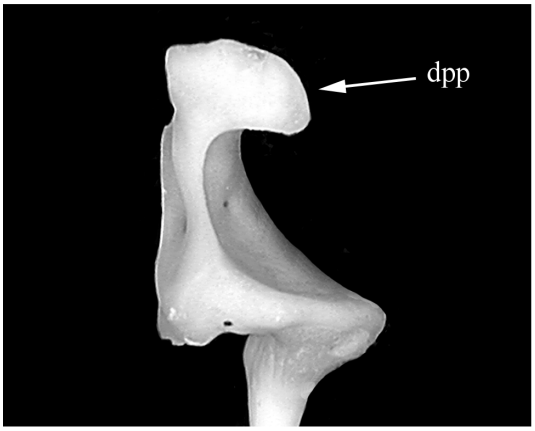
45(0): CM 145580, *cerastes* (rt. maxilla, posterior); dorsal prefrontal process surface roughly as wide as high.



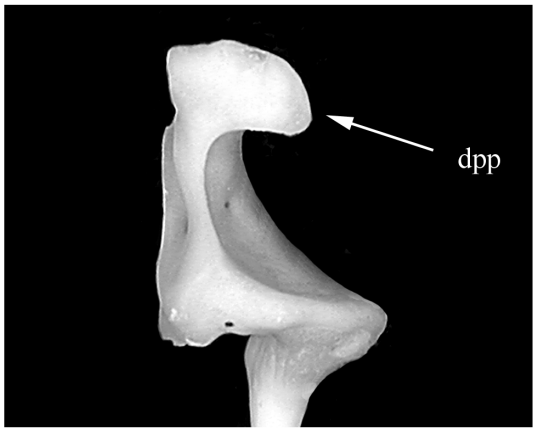
45(1): CJB 490, *ruber* (rt. maxilla, posterior); dorsal prefrontal process surface wider than high.



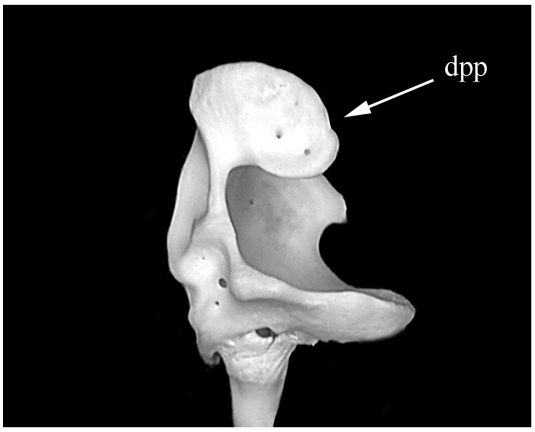
46(0): CJB 1064, *enyo* (rt. maxilla, posterior); entire dorsal edge of dorsal prefrontal process rounded.



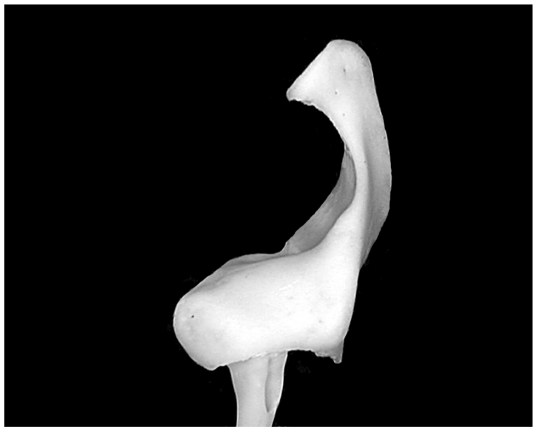
46(1): CJB 1062, *pricei* (rt. maxilla, posterior); medial portion of dorsal edge of dorsal prefrontal process straight.



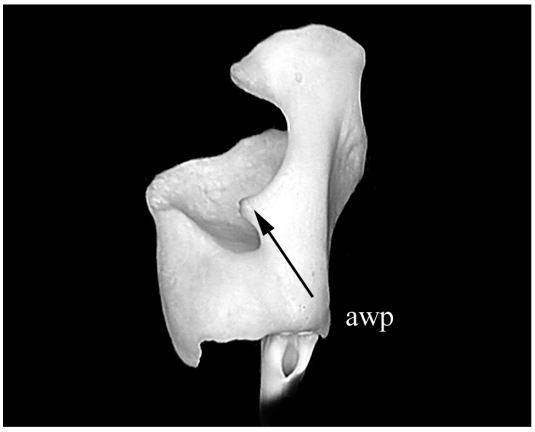
47(0): CJB 1062, *pricei* (rt. maxilla, posterior); ventral edge of dorsal prefrontal process straight.



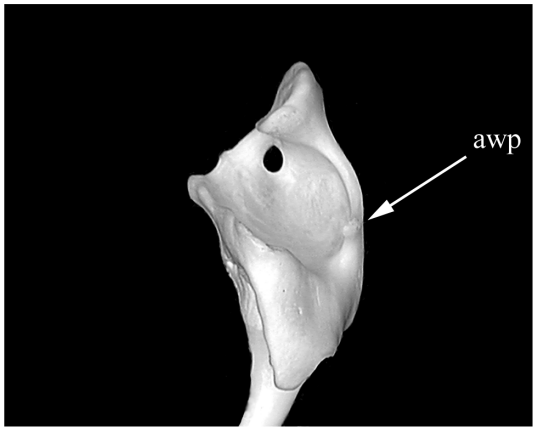
47(1): CJB 490, *ruber* (rt. maxilla, posterior); ventral edge of dorsal prefrontal process curves ventrally, concavity near medial edge.



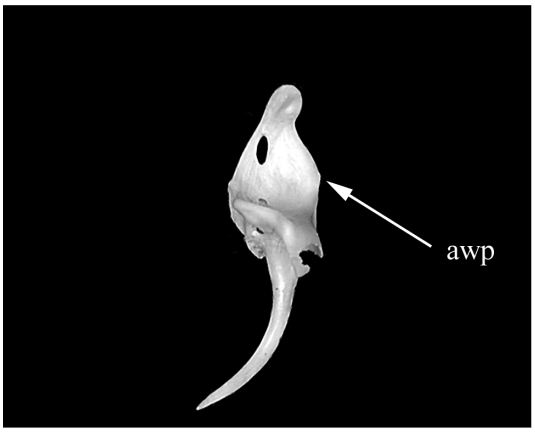
48(0): NAUQSP 14075, *piscivorus* (rt. maxilla, anterior); anteromedial wall process absent.



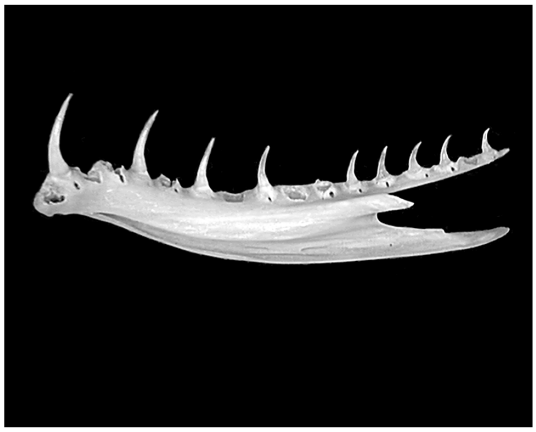
48(1): CJB 490, *ruber* (rt. maxilla, anterior); anteromedial wall process present.



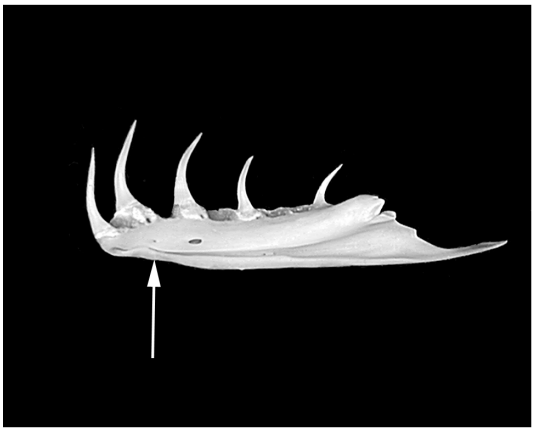
49(0): CJB 490, *ruber* (rt. maxilla, lateral); anteromedial wall process laterally projecting.



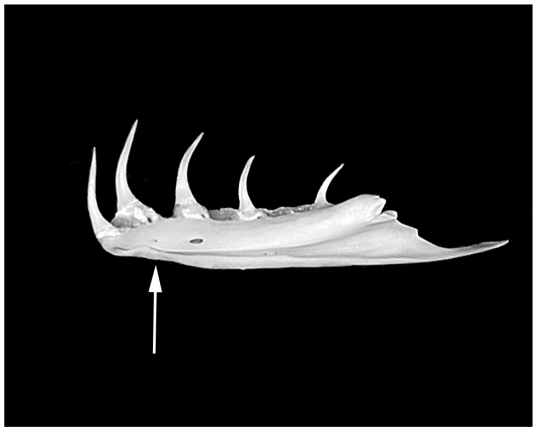
49(0): CJB 715, *contortrix* (rt. maxilla, lateral); anteromedial wall process laterally projecting.



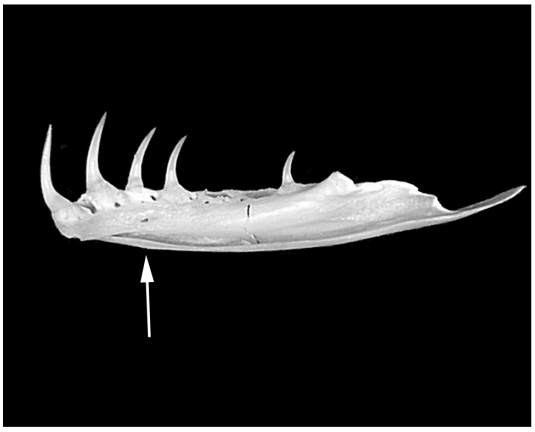
51(0): CJB 692, *bilineatus* (rt. dentary, medial); absence of foramen on medial surface.



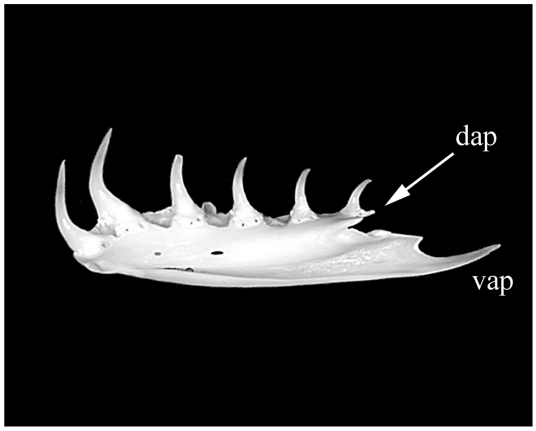
51(1): CJB 490, *ruber* (rt. dentary, medial); presence of foramen on medial surface.



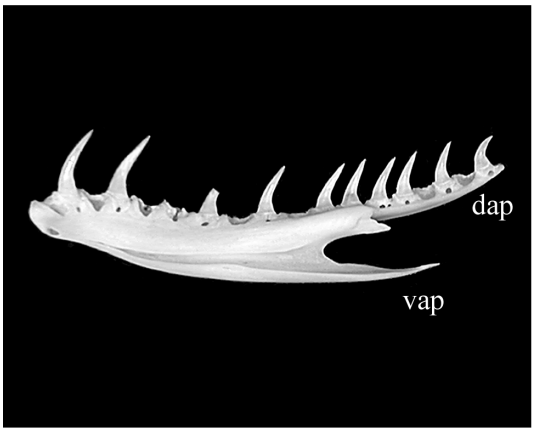
52(0): CJB 490, *ruber* (rt. dentary, medial); medial foramen present under first three tooth sockets.



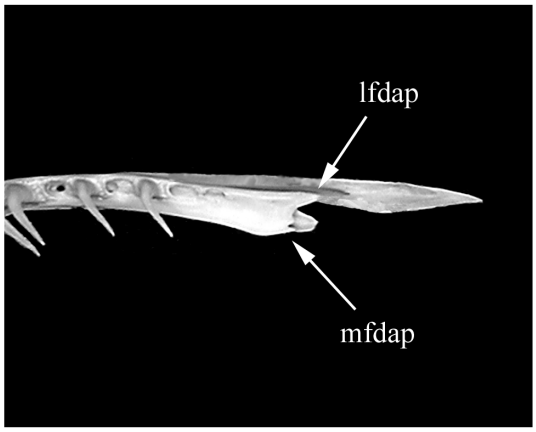
52(1): TJL 930, *polystictus* (rt. dentary, medial); medial foramen present posterior to first three tooth sockets.



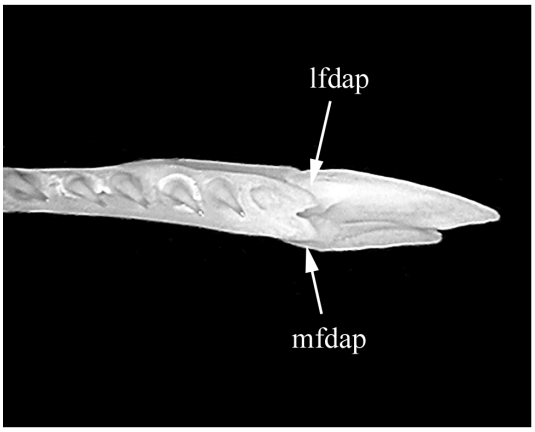
53(0): CJB 001, *atrox* (rt. dentary, medial); ventral articular process longer than dorsal articular process.



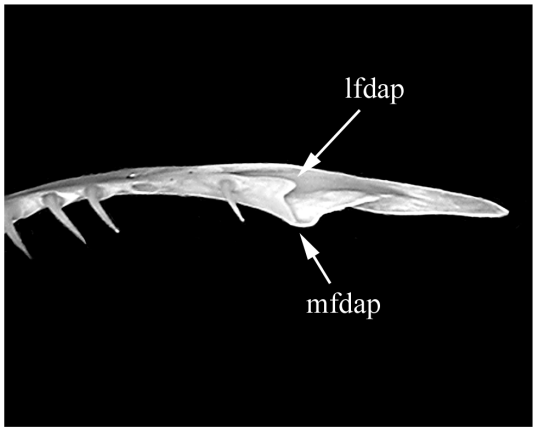
53(1): CJB 508, *piscivorus* (rt. dentary, medial); dorsal articular process longer than ventral articular process.



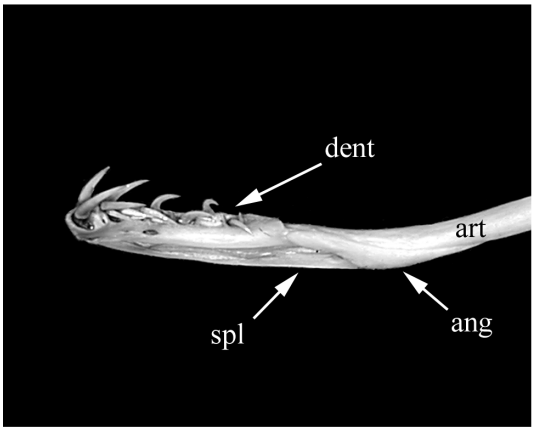
54(0): LSUMZ 29584, *adamanteus* (rt. dentary, dorsal); lateral fork of dorsal articular process longer than medial fork.



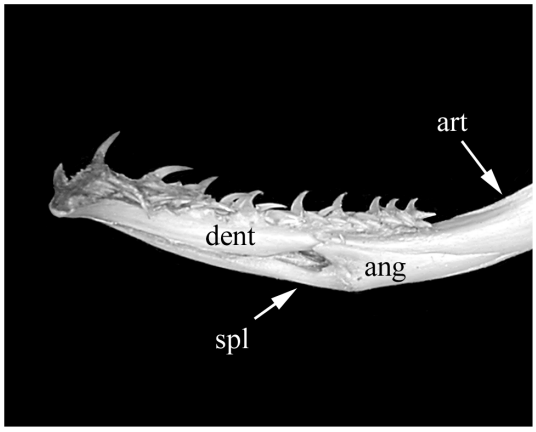
54(1): CJB 1062, *pricei* (rt. dentary, dorsal); lateral and medial forks of dorsal articular process equal lengths.



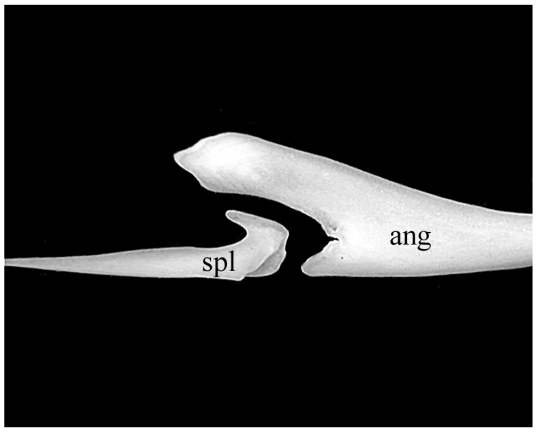
54(2): TJL 930, *polystictus* (rt. dentary, dorsal); medial fork of dorsal articular process longer than lateral fork.



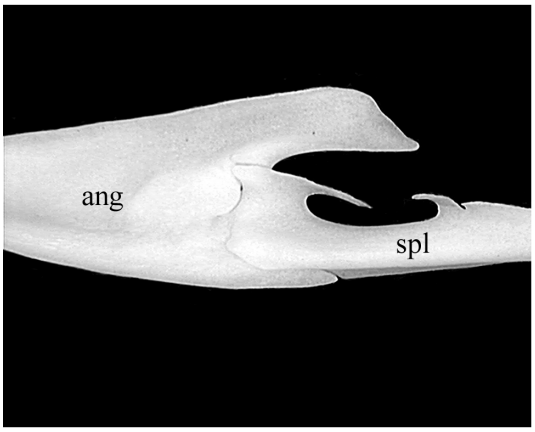
55(0): LSUMZ 55366, *polystictus* (rt. mandible, medial); posteriormost dentary teeth anterior to angular.



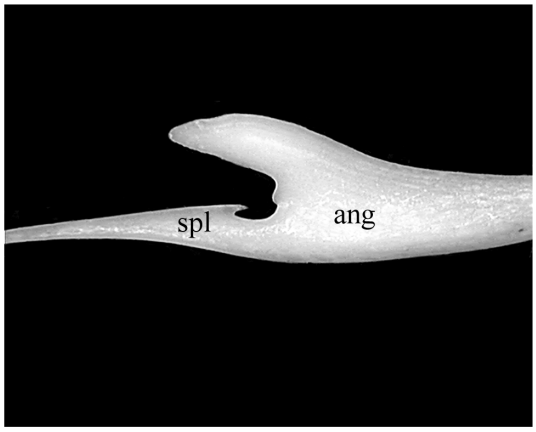
55(1): TJL 539, *piscivorus* (rt. mandible, medial); posteriormost dentary teeth dorsal to angular.



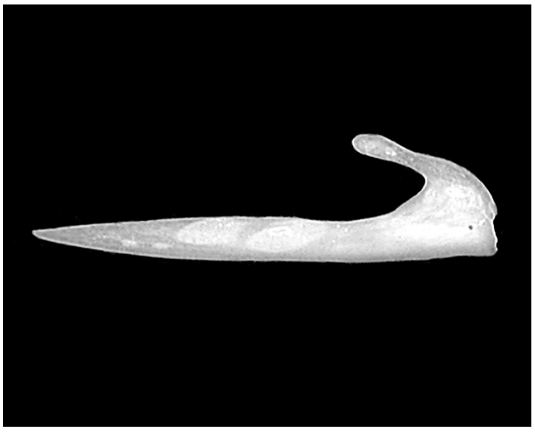
56(0): CJB 001, *atrox* (rt. splenial and angular, medial); splenial and angular totally separate.



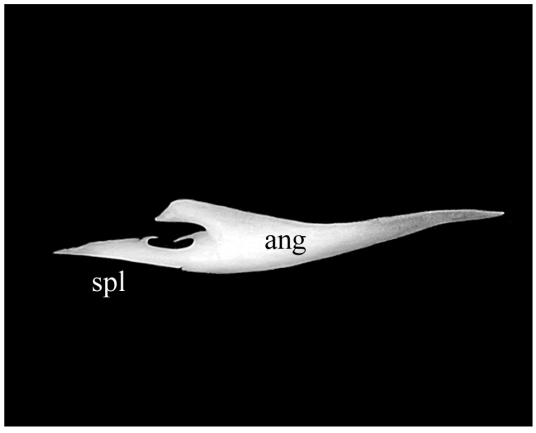
56(1): CJB 490, *ruber* (rt. splenial and angular, lateral); splenial and angular partially fused.



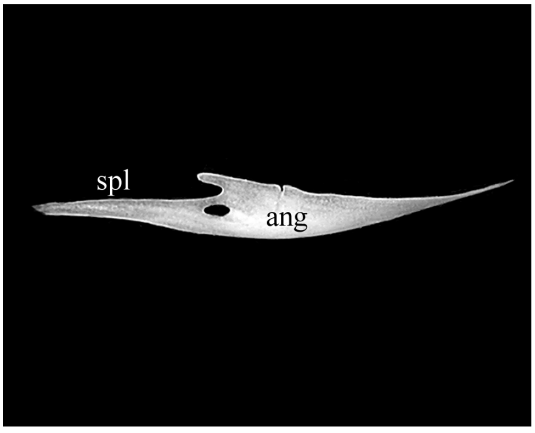
56(2): CJB 697, *molossus* (rt. splenial and angular, medial); splenial and angular completely fused.



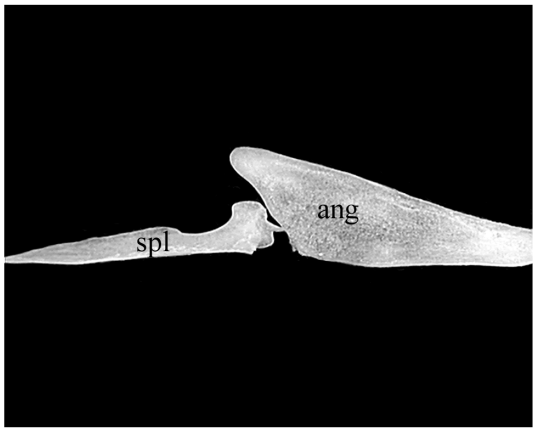
57(0): CJB 692, *bilineatus* (rt. splenial, medial); no foramen enclosed within splenial.



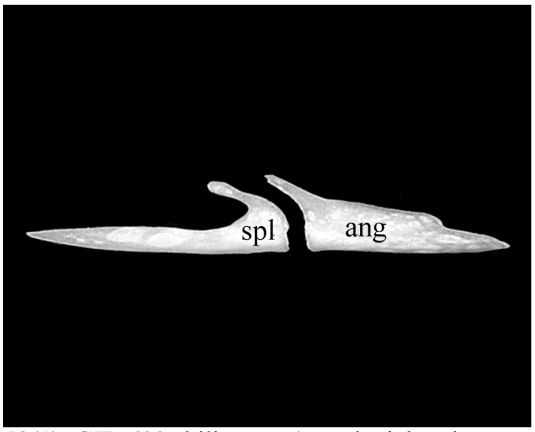
57(1): CJB 490, *ruber* (rt. splenial and angular, medial); dorsal margin of splenial partially forming additional foramen.



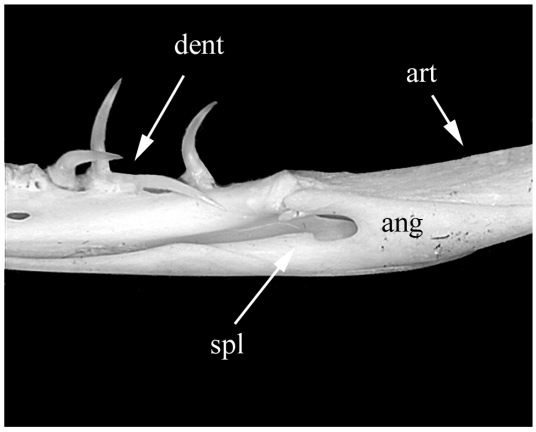
57(2): CJB 691, *catenatus* (rt. splenial and angular, medial); separate foramen entirely enclosed within splenial.



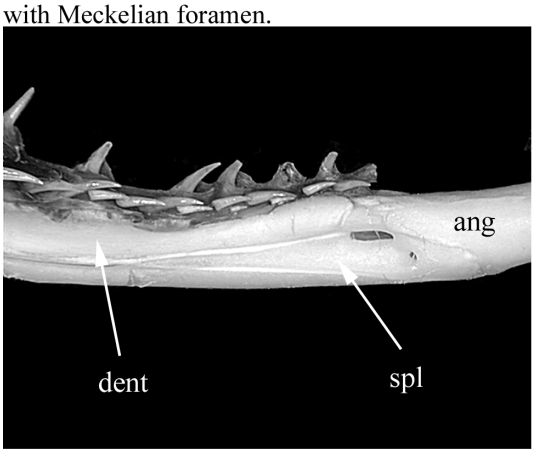
58(0): CJB 001, *atrox* (rt. splenial and angular, medial); angular borders ~1/2 of posterior margin of Meckelian foramen.



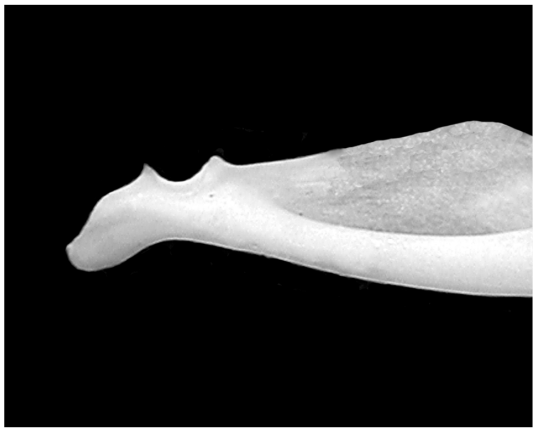
58(1): CJB 692, *bilineatus* (rt. splenial and angular, medial); angular excluded or almost excluded (1/4 posterior margin) from margin with Meckelian foramen.



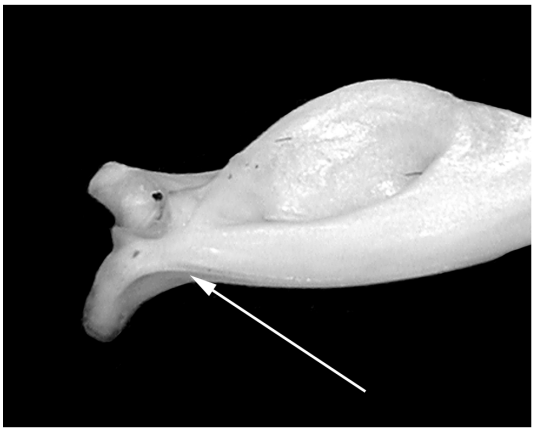
59(0): CJB 070, *durissus* (rt. mandible, medial); splenial attenuate anteriorly, groove in dentary open medially.



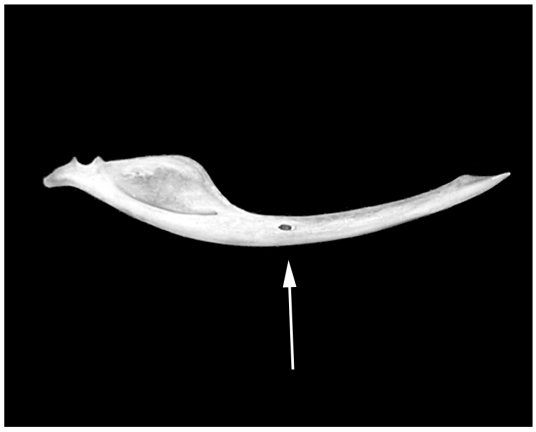
59(1): CAS 14622, *blomhoffii* (rt. mandible, medial); splenial not attenuate anteriorly, contacts dentary to cover portion of groove.



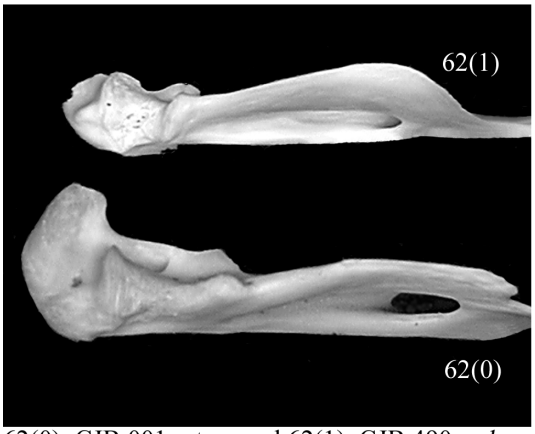
60(0):CJB 258, *basiliscus* (rt. articular, dorsal); thin ventrolateral process ventral to quadrate articulation absent.



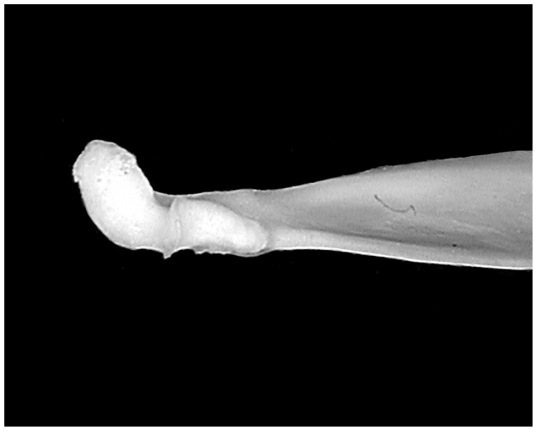
60(0):CJB 001, *atrox* (rt. articular, dorsal); thin ventrolateral process ventral to quadrate articulation present.



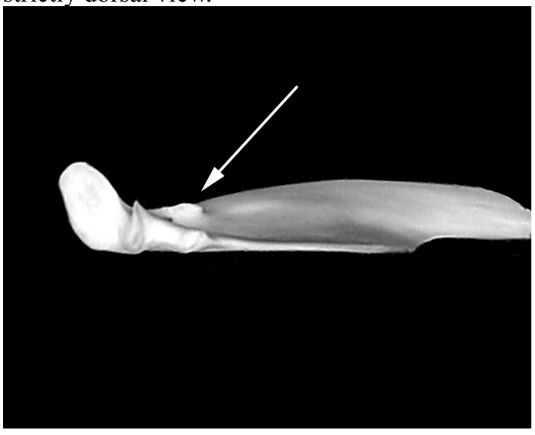
61(0): CJB 001, *atrox* (rt. articular, lateral); anterior articular foramen present anterior to anteriormost extension of dorsal projection.



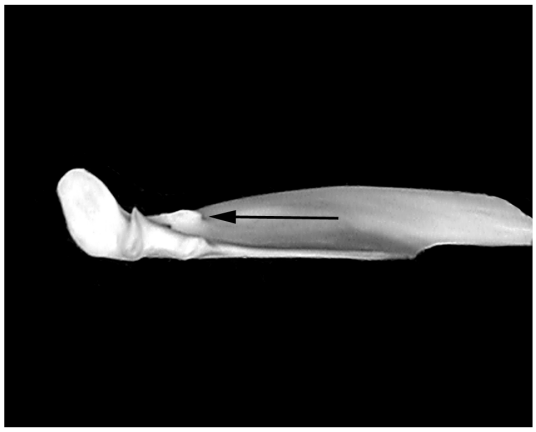
62(0): CJB 001, *atrox* and 62(1): CJB 490, *ruber* (both rt. articulars, dorsolateral); posterior Meckelian foramen: visible or not visible from strictly dorsal view.



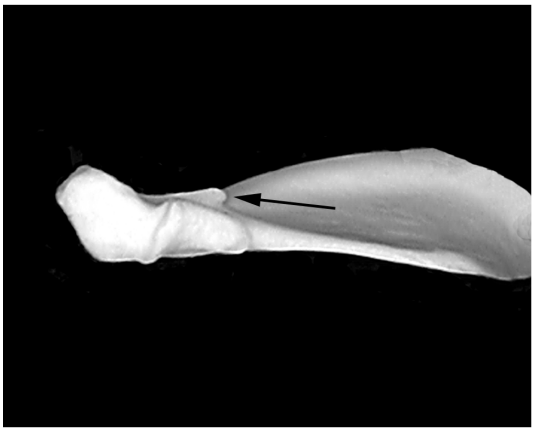
63(0): TJL 814, *lepidus* (rt. articular, dorsal); medial process absent, ventral to quadrate articulation.



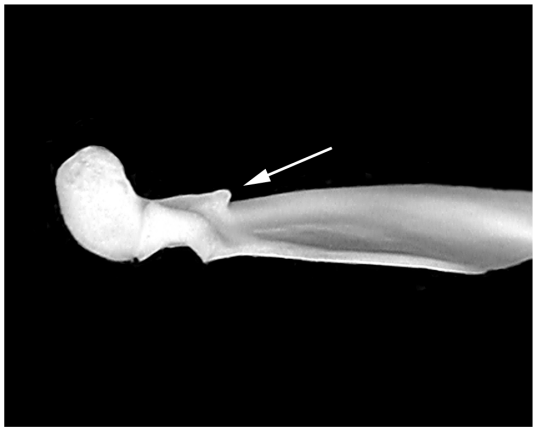
63(1): LSUMZ 83787, *willardi* (rt. articular, dorsal); medial process present, ventral to quadrate articulation.



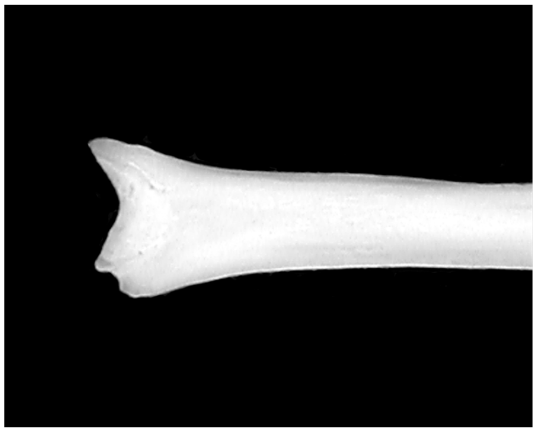
64(0): CJB 001, *atrox* (rt. articular, dorsal); medial process ventral to quadrate articulation present as small rounded bump.



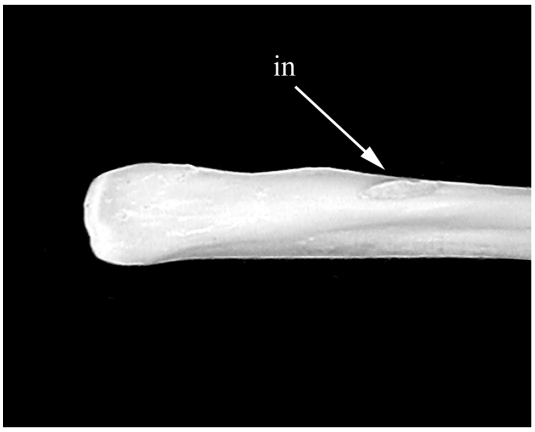
64(1): CJB 699, *cerastes* (rt. articular, dorsal); medial process ventral to quadrate articulation present as small pointed projection.



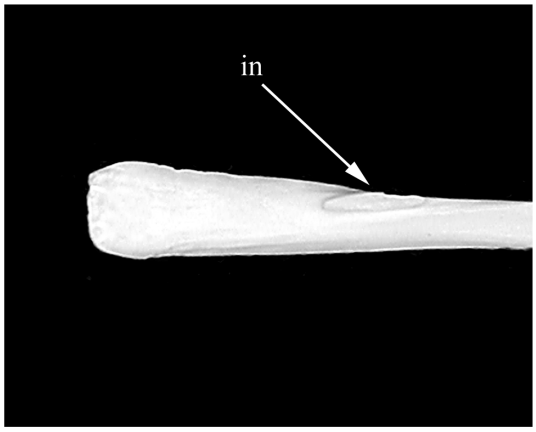
64(2): TJL 930, *polystictus* (rt. articular, dorsal); medial process ventral to quadrate articulation present as distinct pointed anteromedial process.



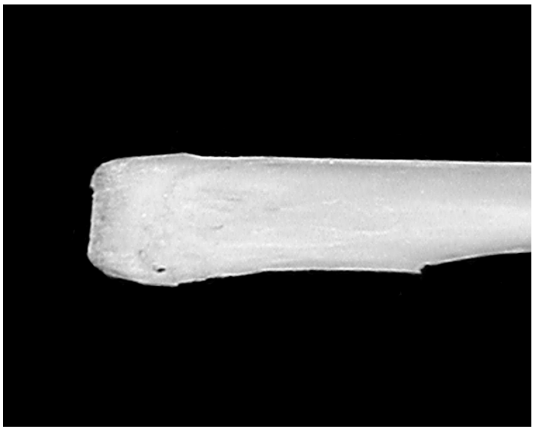
65(1): CJB 001, *atrox* (rt. quadrate, dorsal); posterior process of quadrate forked.



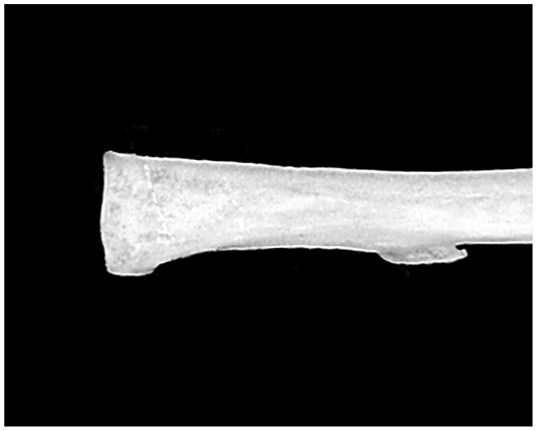
66(0): CJB 258, *basiliscus* (rt. quadrate, dorsal); anterior 1/3 of bone equal width, narrows at intercalary nodule.



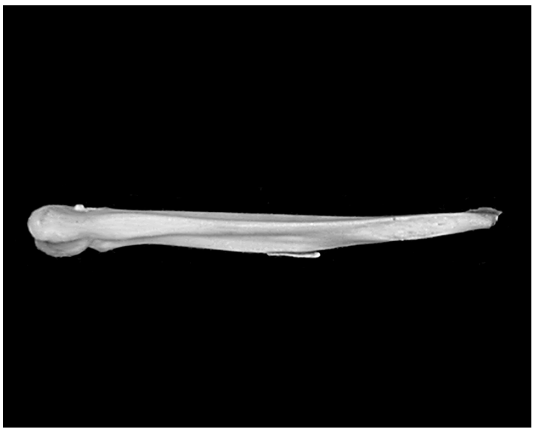
66(0): CJB 001, *atrox* (rt. quadrate, dorsal); anterior 1/3 of bone narrows well before intercalary nodule.



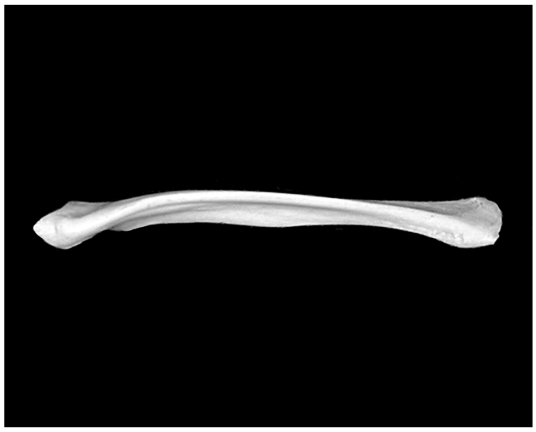
67(0): CJB 490, *ruber* (rt. quadrate, dorsal); anterior margin rounded.



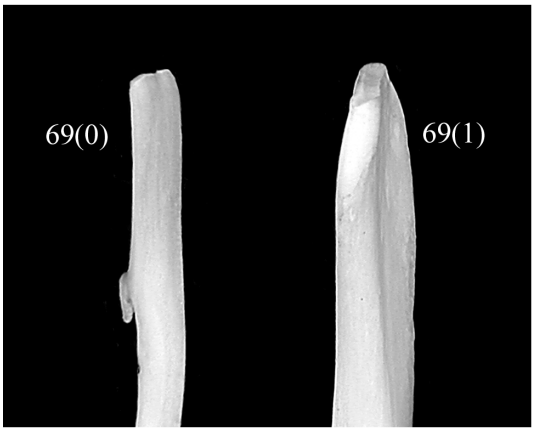
67(1): CJB 690, *miliarius* (rt. quadrate, dorsal); anterior margin squared off.



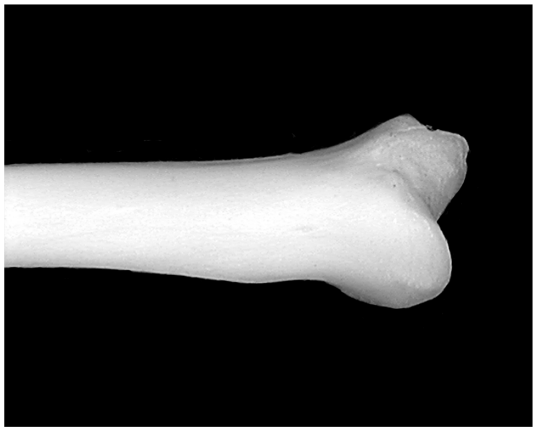
68(0): CJB 574, *atrox* (rt. quadrate, lateral); lateral margin mostly straight, not bowed dorsally.



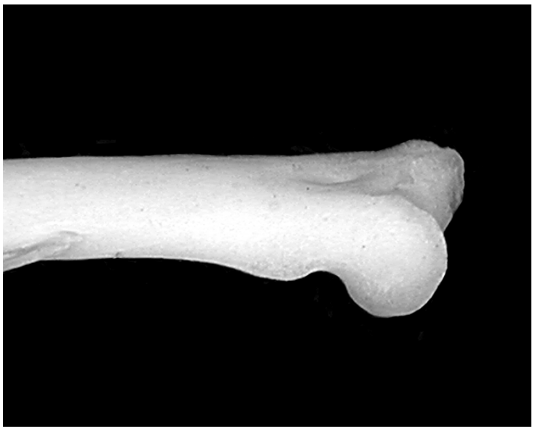
68(1):LSUMZ 29347, *durissus* (rt. quadrate, lateral); lateral margin rounded, bowed dorsally.



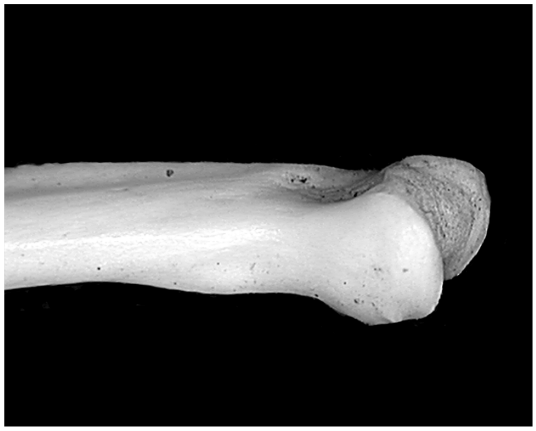
69(0): CJB 1062, *pricei* and 69(1): CJB 490, *ruber* (both rt. quadrate, dorsal); dorsal surface of anterior end relatively flat vs. concave.



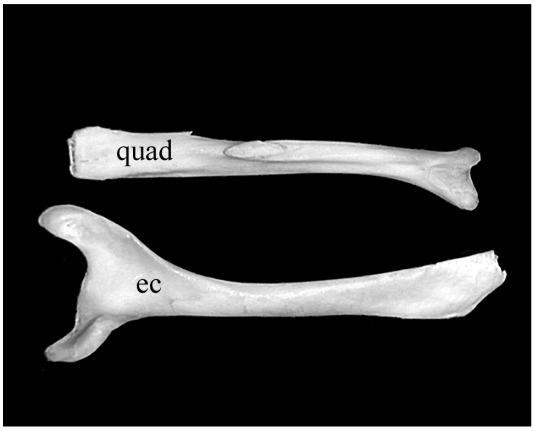
70(0): LSUMZ 29583, *atrox* (rt. quadrate, dorsal); dorsal surface relatively flat proximal to articulation facet.



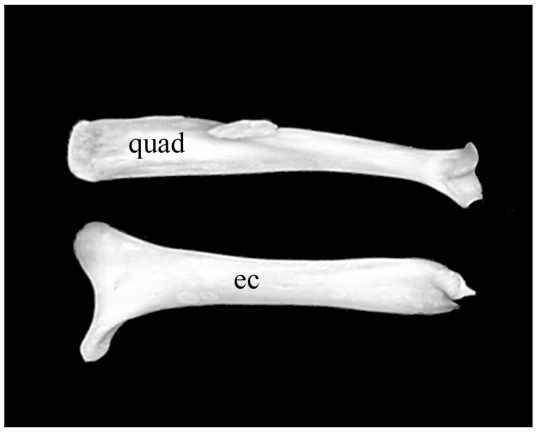
70(1): CJB 001, *atrox* (rt. quadrate, dorsal); dorsal surface shallowly concave proximal to articulation facet.



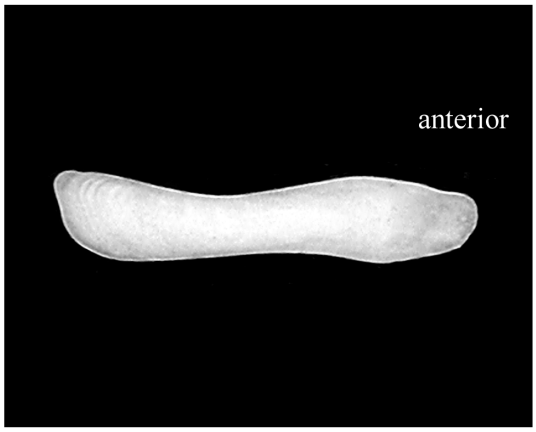
70(2): LSUMZ 34173, *adamanteus* (rt. quadrate, dorsal); dorsal surface deeply concave proximal to articulation facet.



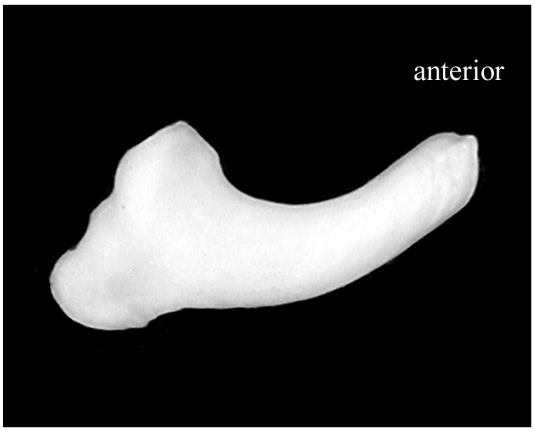
71(0): CJB 574, *atrox* (rt. quadrate and ectopterygoid, ventral/dorsal); quadrate shorter than ectopterygoid.



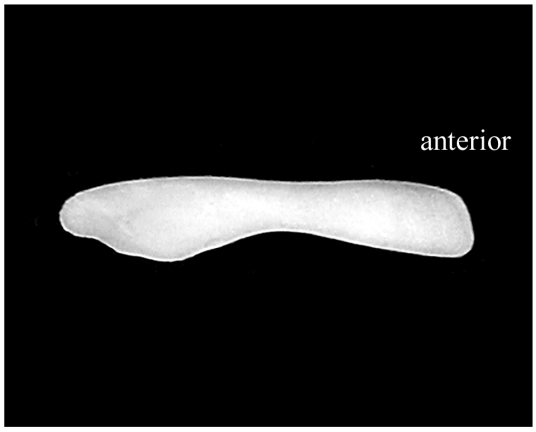
71(1): CJB 692, *bilineatus* (rt. quadrate and ectopterygoid, ventral/dorsal); quadrate equal to or longer than ectopterygoid.



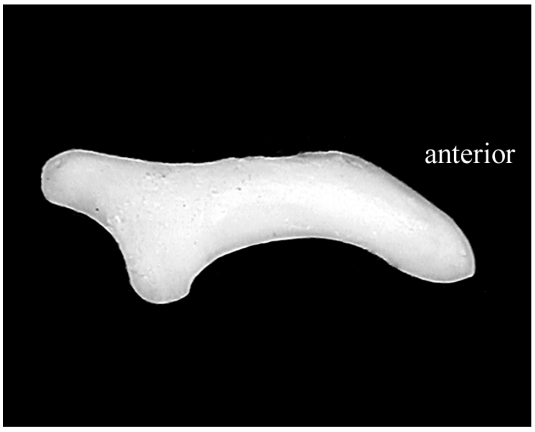
72(0): NAUQSP 14076, *contortrix* (rt. supratemporal, dorsal); caudal end widened, but lacking distinct projection.



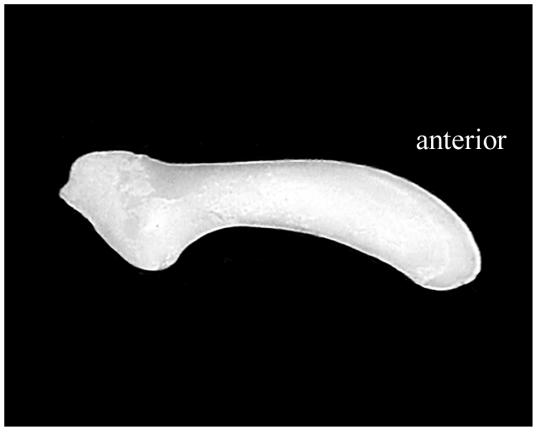
72(1): CJB 001, *atrox* (left supratemporal, dorsal); caudal end widened with posterolateral projection.



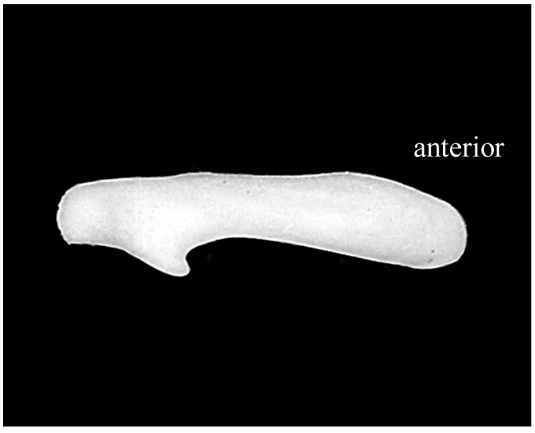
73(0): CJB 715, *contortrix* (rt. supratemporal, dorsal); small posterolateral projection.



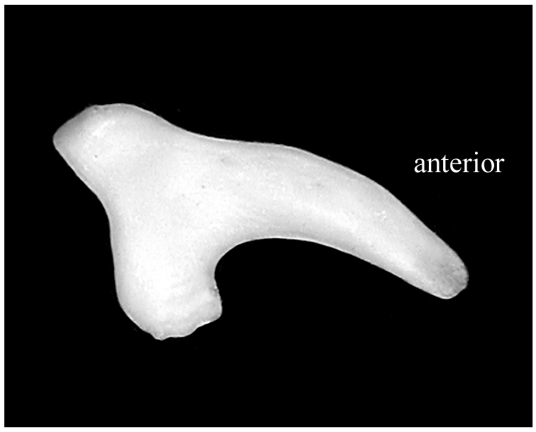
73(1): NAUQSP 14086, *basiliscus* (rt. supratemporal, dorsal); large posterolateral projection.



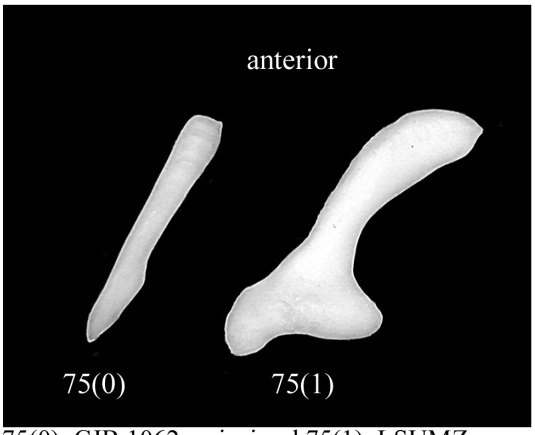
74(0): TJL 930, *polystictus* (rt. supratemporal, dorsal); posterolateral process rounded.



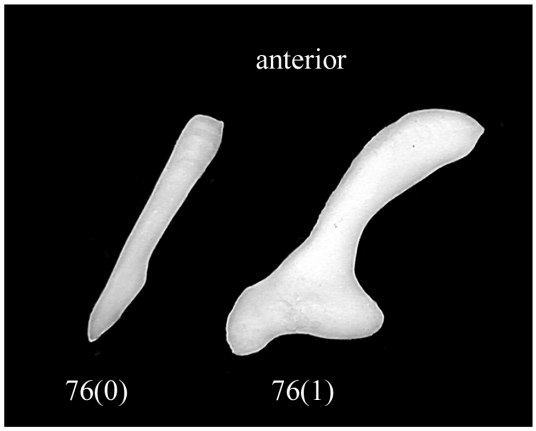
74(1): CJB 1060, *lepidus* (rt. supratemporal, dorsal); posterolateral process pointed.



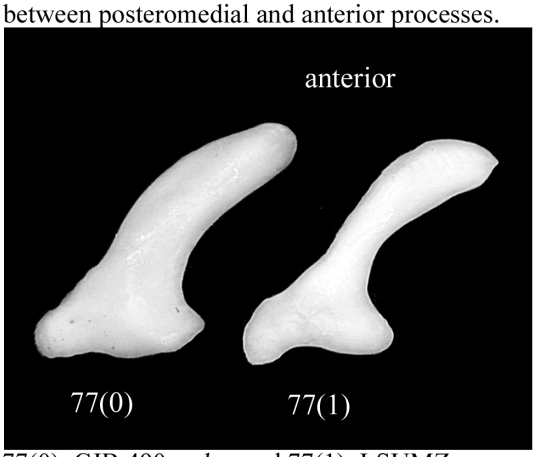
74(2): CJB 001, *atrox* (rt. supratemporal, dorsal); posterolateral process squared.



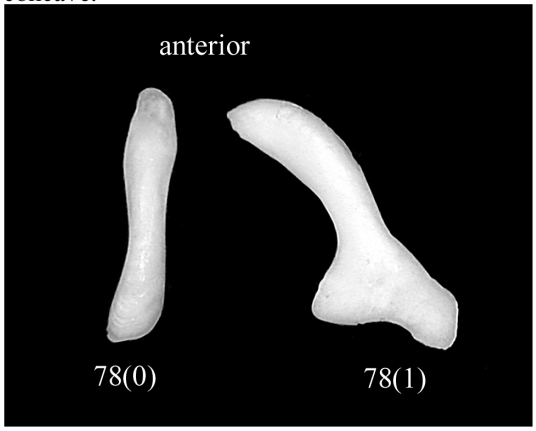
75(0): CJB 1062, *pricei* and 75(1): LSUMZ 10340, *horridus* (both rt. supratemporal, dorsal); medial margin without or with definite concavity between posteromedial and anterior processes.



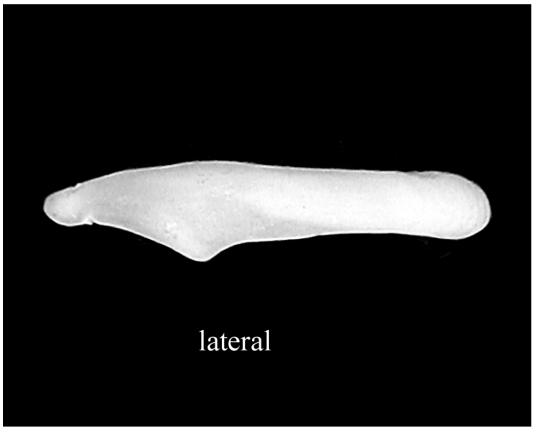
76(0): CJB 1062, *pricei* and 76(1): LSUMZ 10340, *horridus* (both rt. supratemporal, dorsal); lateral margin mostly straight vs. lateral margin concave.



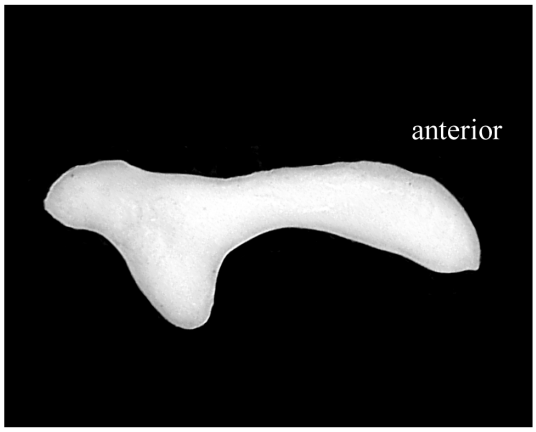
77(0): CJB 490, *ruber* and 77(1): LSUMZ 10340, *horridus* (both rt. supratemporal, dorsal); width posterior base of anterior process equal to anterior end vs. narrower than anterior end.



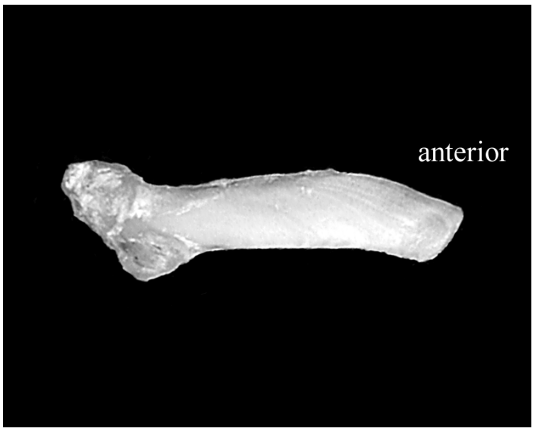
78(0): NAUQSP 14086, *basiliscus* and 78(1): LSUMZ 10340, *horridus* (both rt. supratemporal, dorsal); posterior processes without distinct processes vs. presence of at least one process.



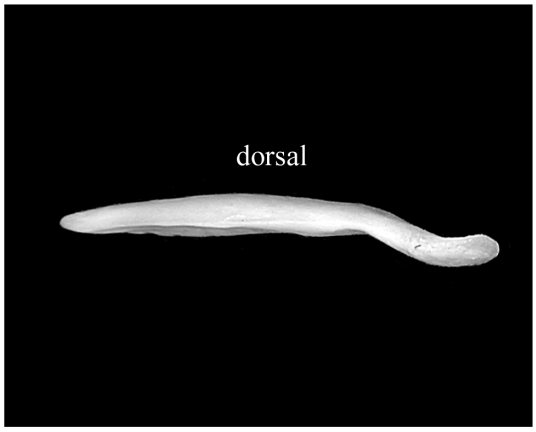
79(0): CJB 508, *piscivorus* (rt. supratemporal, dorsal); only lateral posterior process distinct.



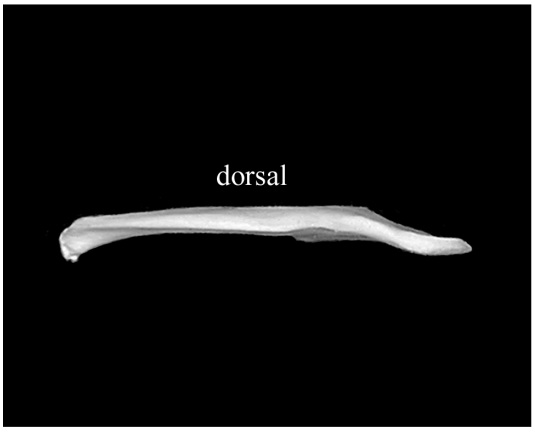
79(1): LSUMZ 10340, *horridus* (rt. supratemporal, dorsal); both medial and lateral posterior processes distinct.



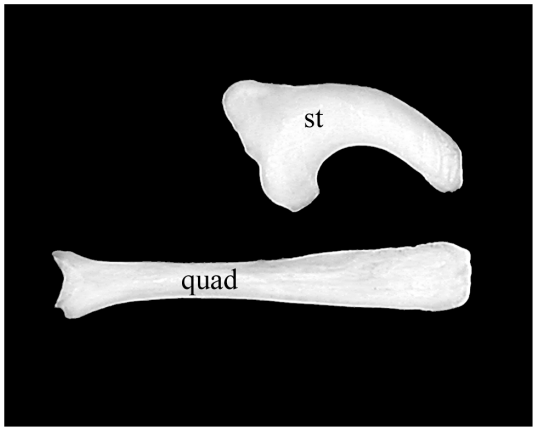
79(2): UTEP 946, *polystictus* (rt. supratemporal, dorsal); only medial posterior process distinct.



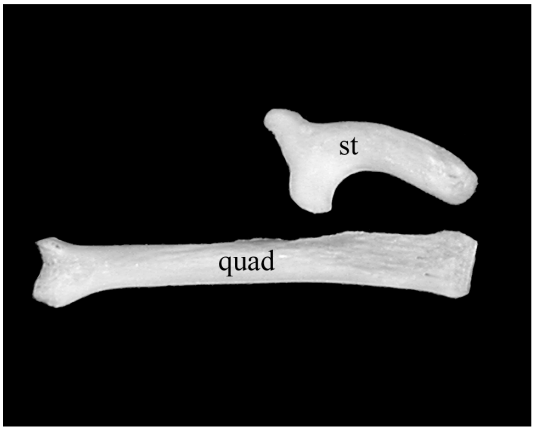
80(0): LSUMZ 29347, *horridus* (rt. supratemporal, lateral); rounded dorsal surface.



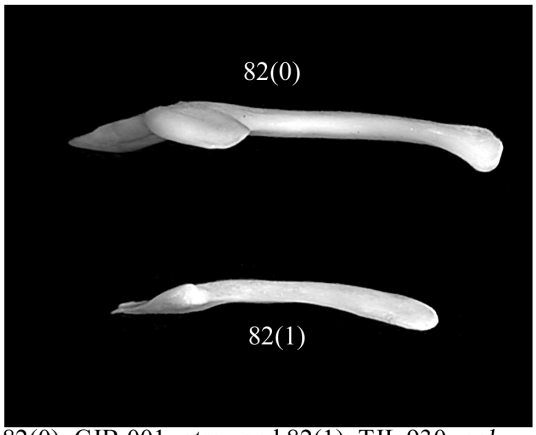
80(1): CJB 001, *atrox* (rt. supratemporal, lateral); flat dorsal surface.



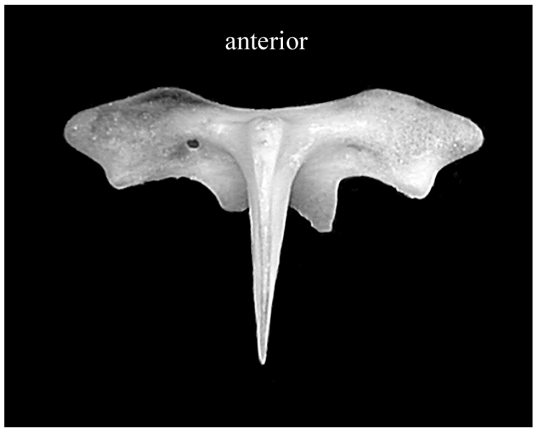
81(0): CJB 001, *atrox* (rt. supratemporal and quadrate, dorsal); supratemporal greater than 50% quadrate length.



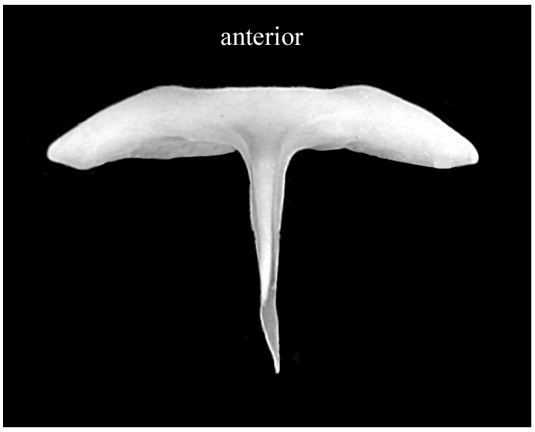
81(1): CJB 573, *atrox* (rt. supratemporal and quadrate, dorsal); supratemporal less than or equal to 50% quadrate length.



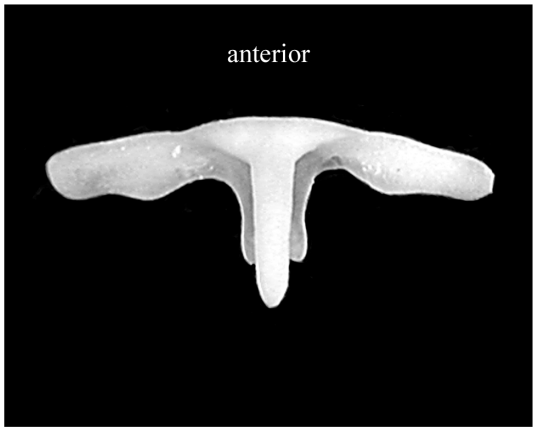
82(0): CJB 001, *atrox* and 82(1): TJL 930, *polystictus* (both rt. supratemporal, lateral); all three processes point ventrally (oblique) vs. lateral process points dorsally (oblique).



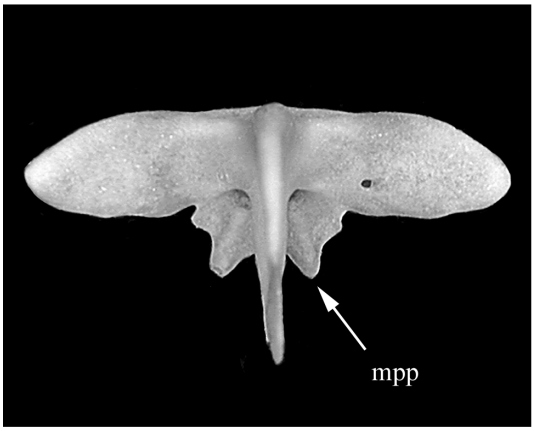
83(0): LSUMZ 29347, *durissus* (premaxilla, dorsal); middle 1/3 of anterior edge of transverse bar concave (in dorsal view).



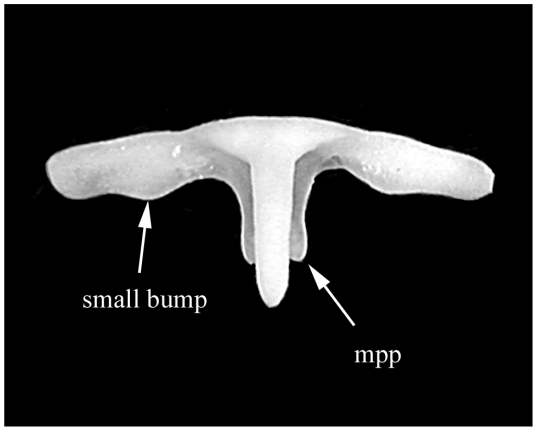
83(1): CJB 001, *atrox* (premaxilla, dorsal); middle 1/3 of anterior edge of transverse bar straight (in dorsal view).



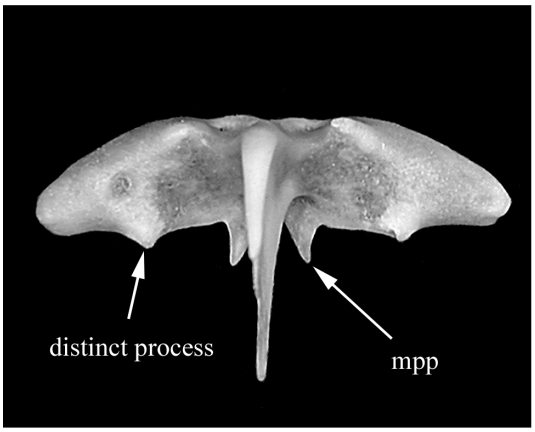
83(2): CJB 1062, *pricei* (premaxilla, dorsal); middle 1/3 of anterior edge of transverse bar convex.



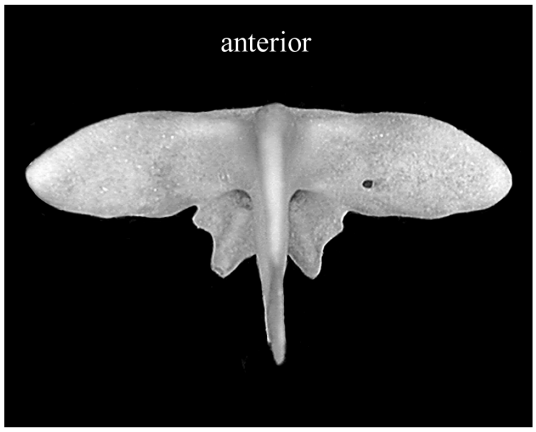
84(0): CJB 573, *atrox* (premaxilla, dorsal); posterior margin of ventral edge smooth (exclusive of median palatal processes).



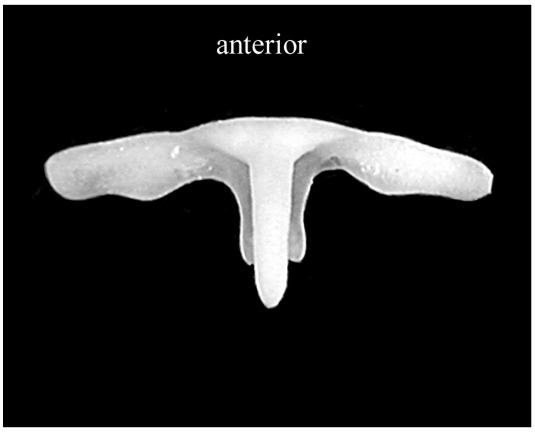
84(1): CJB 1062, *pricei* (premaxilla, dorsal); posterior margin of ventral edge with small bump(s) (exclusive of median palatal processes).



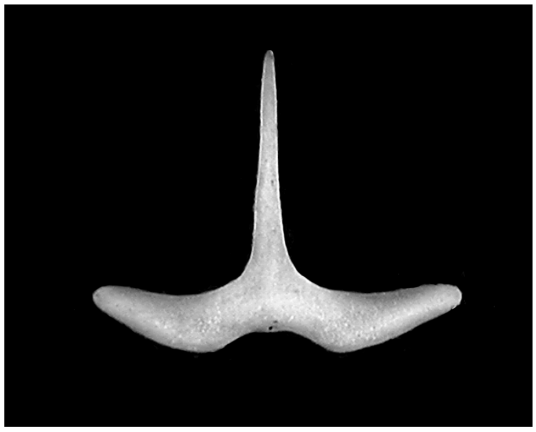
84(2): LSUMZ 34177, *adamanteus* (premaxilla, dorsal); posterior margin of ventral edge with distinct small posterior processes (exclusive of median palatal processes).



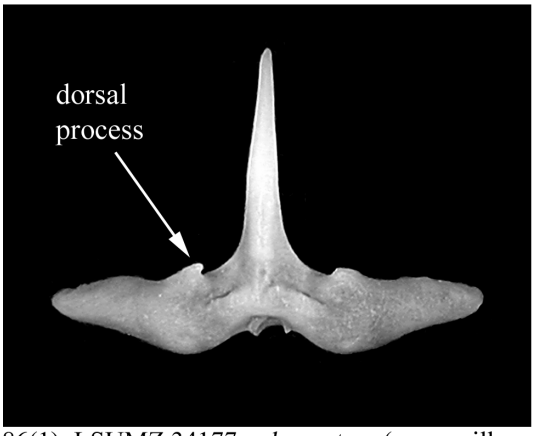
85(0): CJB 573, *atrox* (premaxilla, dorsal); posterior margin nearly perpendicular to the midline.



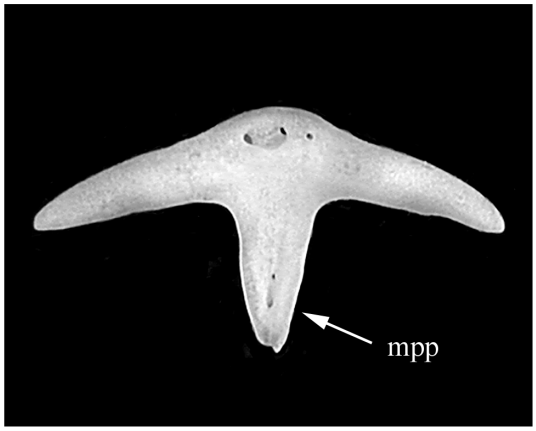
85(1): CJB 1062, *pricei* (premaxilla, dorsal); posterior margin slopes posteriorly.



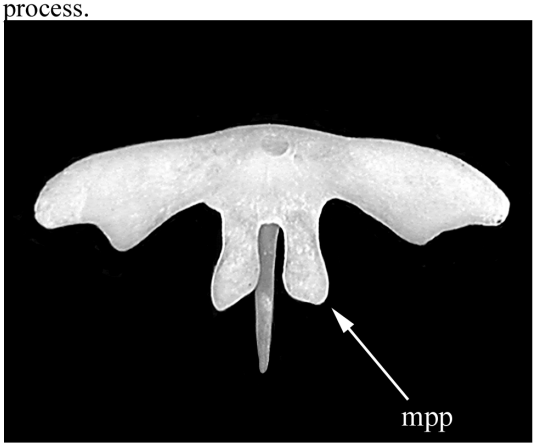
86(0): CJB 573, *atrox* (premaxilla, anterior); dorsal margin of anterior edge without small dorsal processes adjacent to ascending process.



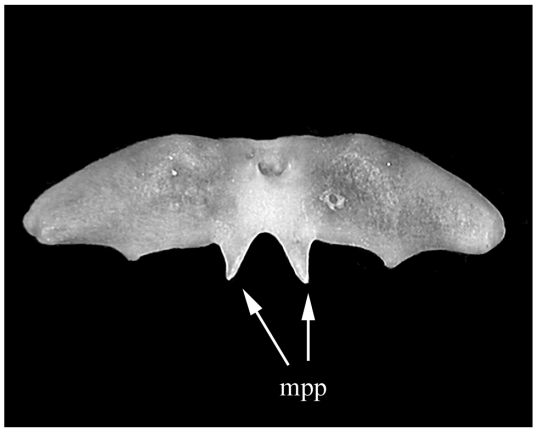
86(1): LSUMZ 34177, *adamanteus* (premaxilla, anterior); dorsal margin of anterior edge with small dorsal processes adjacent to ascending process.



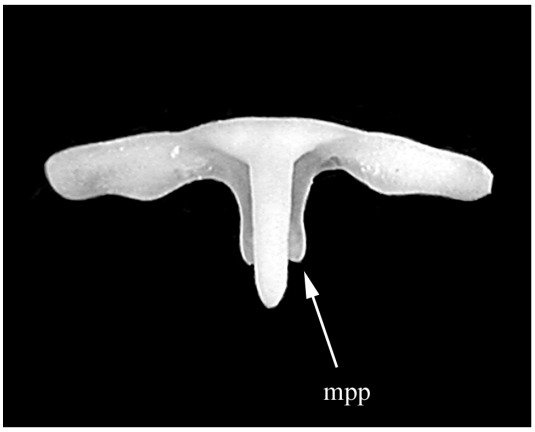
87(0): CJB 715, *contortrix* (premaxilla, ventral); two separate posterior projecting processes of median palatal process absent.



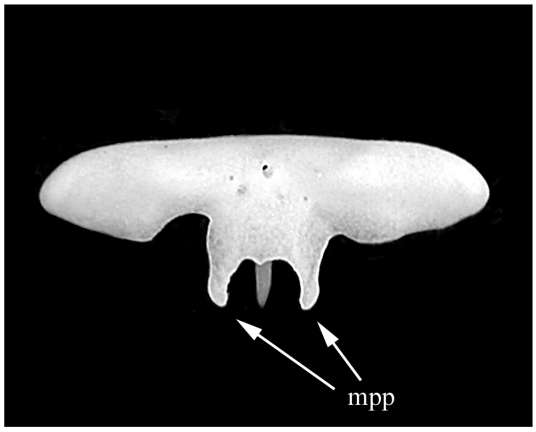
87(1): TJL 930, *polystictus* (premaxilla, ventral); two separate posterior projecting processes of median palatal process present.



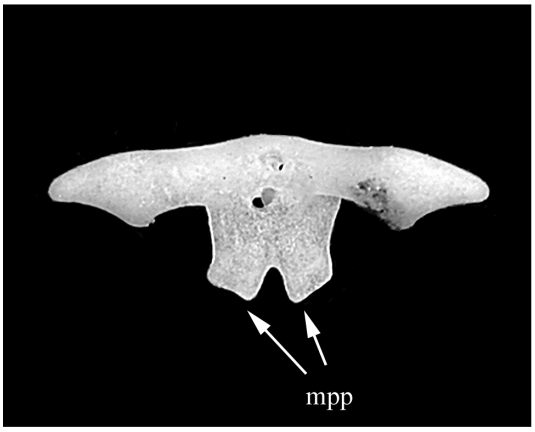
88(0): LSUMZ 34177, *adamanteus* (premaxilla, ventral); separate pointed posterior projecting processes of median palatal process.



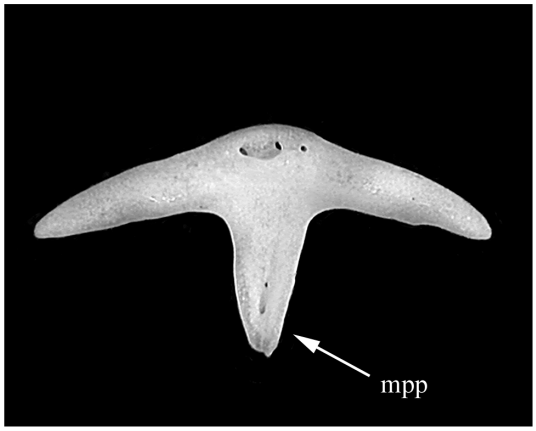
88(1): CJB 1062, *pricei* (premaxilla, dorsal); separate rounded posterior projecting processes of median palatal process.



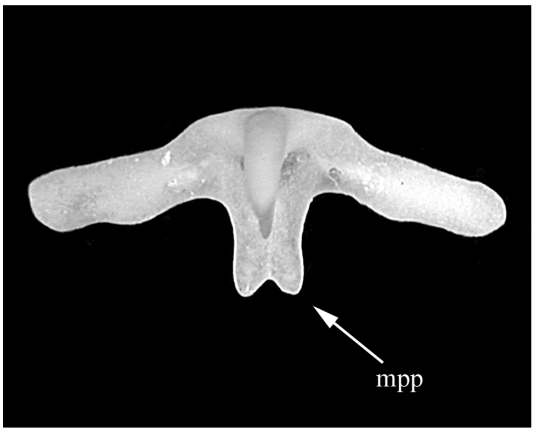
88(2): CJB 650, *cerastes* (premaxilla, ventral); separate lobed posterior projecting processes of median palatal process.



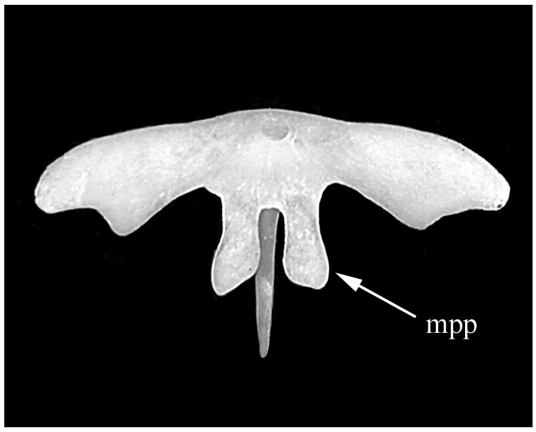
88(3): UMMZ 183544, *lepidus* (premaxilla, ventral); separate squared posterior projecting processes of median palatal process.



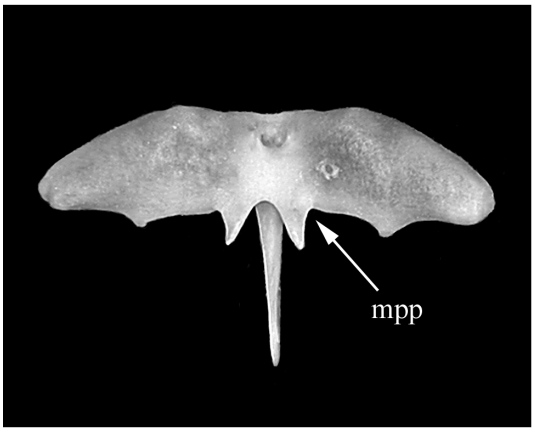
89(0): CJB 715, *contortrix* (premaxilla, ventral); median palatal process, paired processes absent or indistinct.



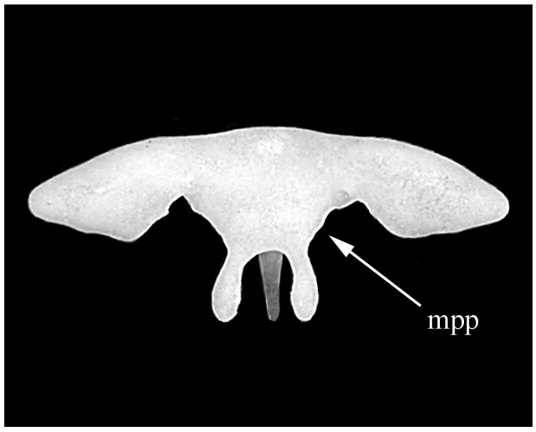
89(1): CJB 1062, *pricei* (premaxilla, ventral); median palatal process, paired processes small but separated.



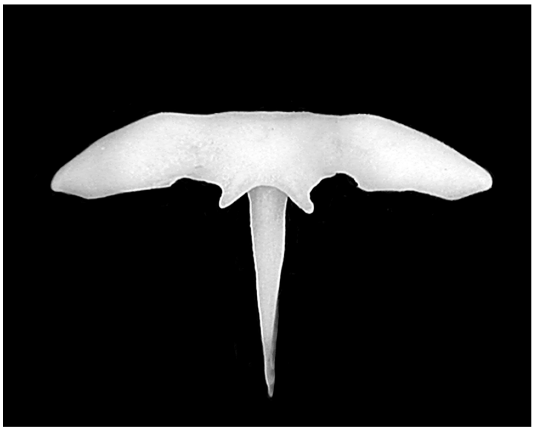
89(2): TJL 930, *polystictus* (premaxilla, ventral); median palatal process, paired processes large and very distinct.



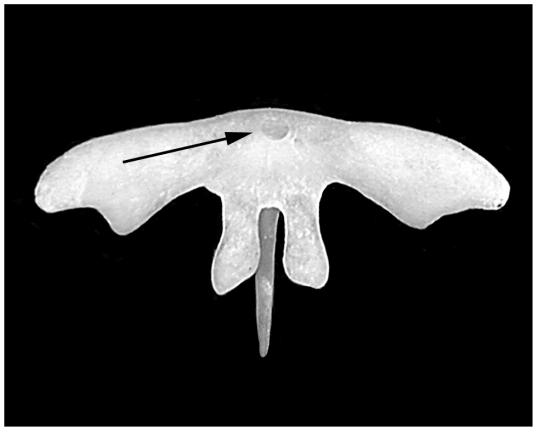
90(0): LSUMZ 34177, *adamanteus* (premaxilla, ventral); median palatal process, shared horizontal plate does not extend posteriorly.



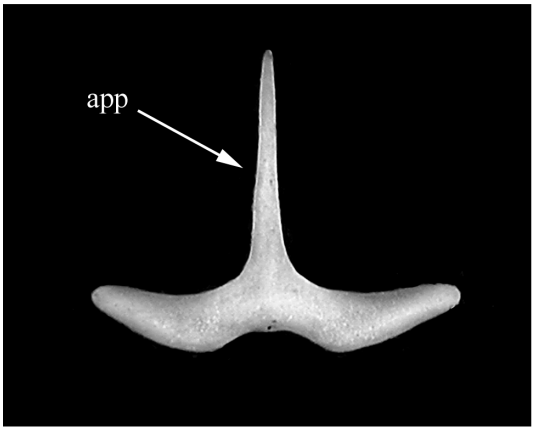
90(1): LSUMZ 10340, *horridus* (premaxilla, ventral); median palatal process, shared horizontal plate extends posteriorly.



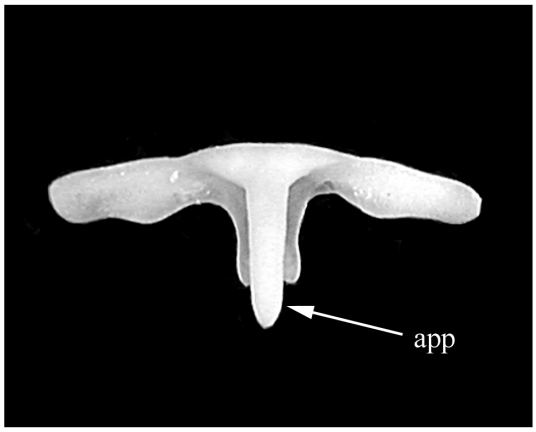
91(0): CJB 001, *atrox* (premaxilla, ventral); absence of median fenestra on ventral surface of transverse bar.



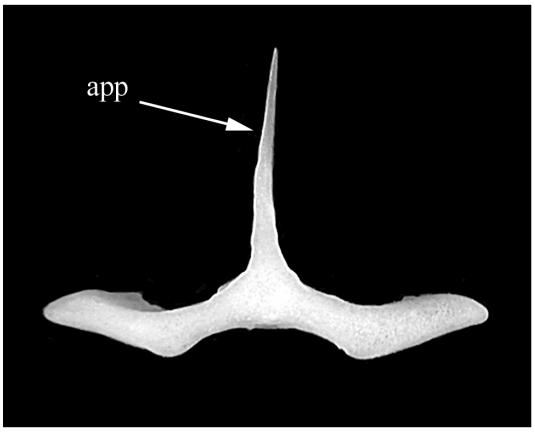
91(1): TJL 930, *polystictus* (premaxilla, ventral); presence of median fenestra on ventral surface of transverse bar.



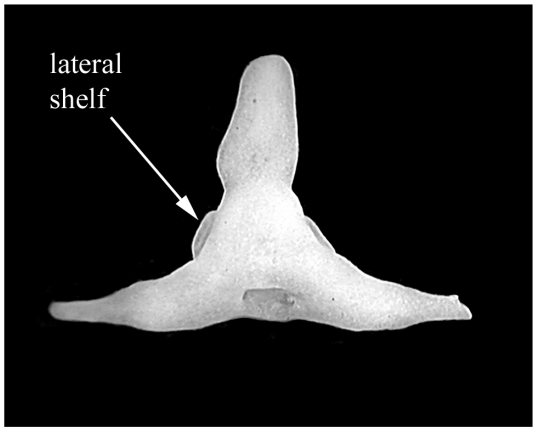
92(0): CJB 573, *atrox* (premaxilla, anterior); ascending process of premaxilla, anterior edge narrows as it ascends posteriorly.



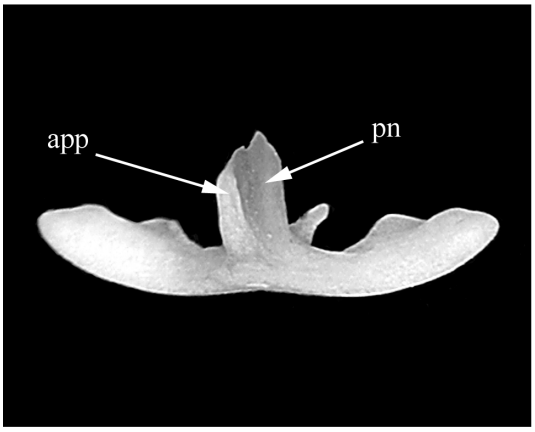
92(1): CJB 1062, *pricei* (premaxilla, dorsal); ascending process of premaxilla, anterior edge does not narrows as it ascends posteriorly.



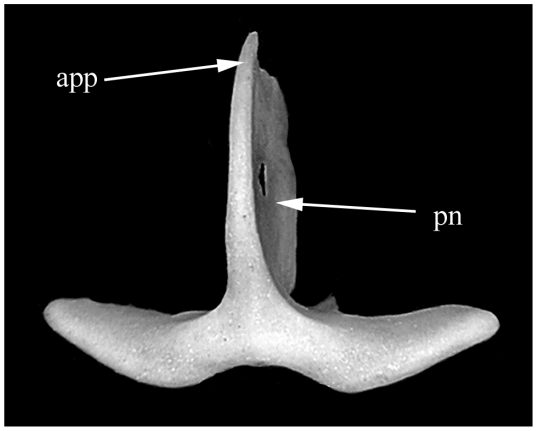
93(0): CJB 001, *atrox* (premaxilla, anterior); ascending process of premaxilla without lateral shelves.



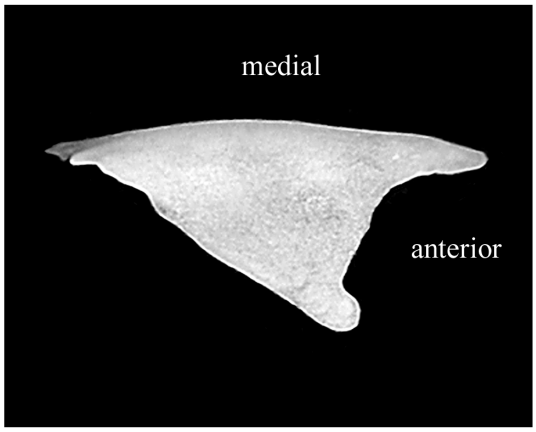
93(1): CJB 692, *bilineatus* (premaxilla, anterior); ascending process of premaxilla with lateral shelves.



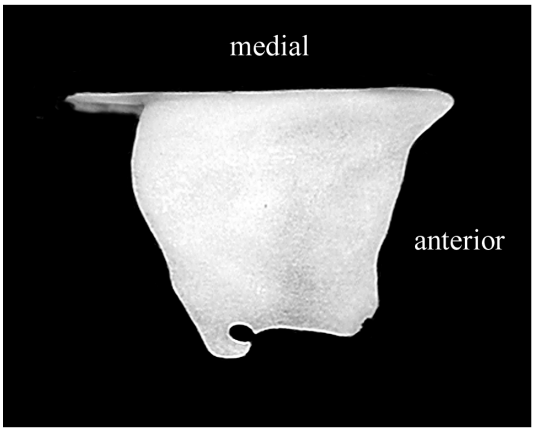
94(0): CJB 001, *atrox* (premaxilla, dorsolateral); ascending process does not extend posterior to posterodorsal margin of processus nasalis.



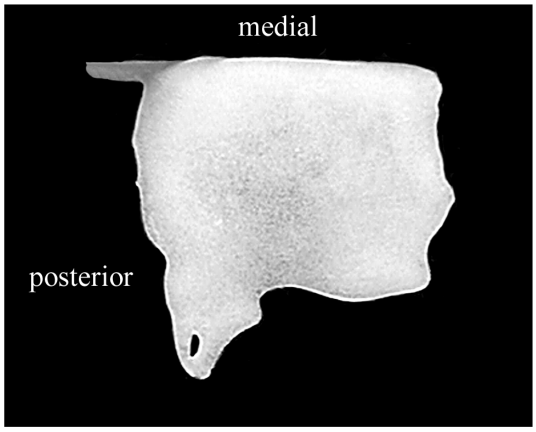
94(0): CJB 573, *atrox* (premaxilla, dorsolateral); ascending process extends posterior to posterodorsal margin of processus nasalis.



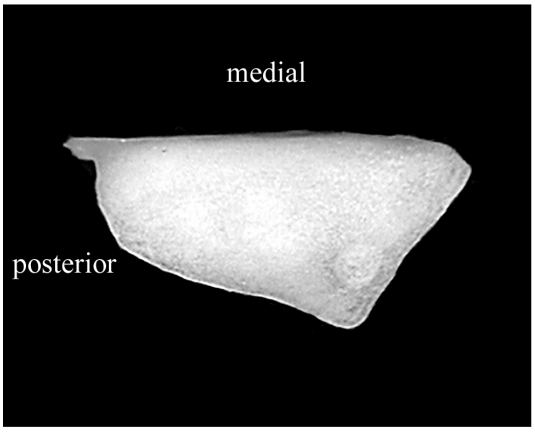
95(0): CJB 692, *bilineatus* (rt. nasal, dorsal); triangular dorsal shelf.



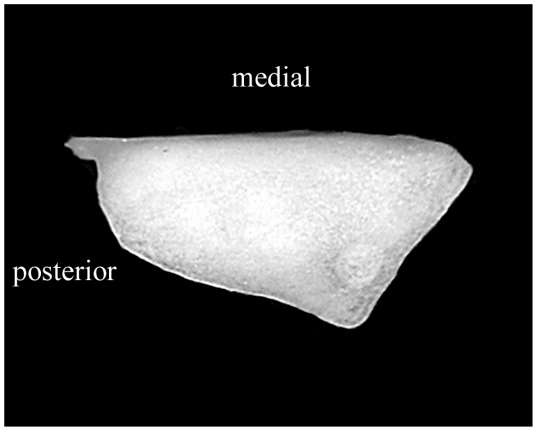
95(1): CJB 001, *atrox* (rt. nasal, dorsal); dorsal shelf not triangular.



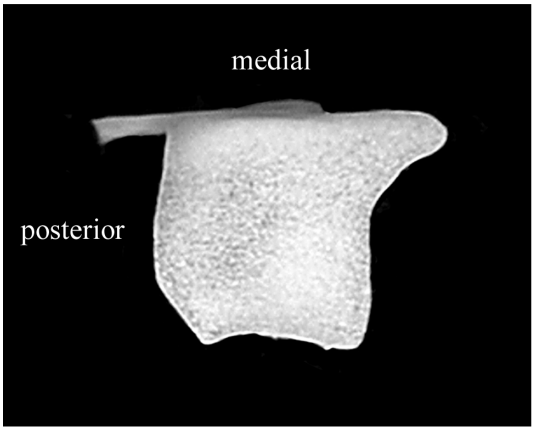
96(0): CJB 490, *ruber* (rt. nasal, dorsal); dorsal shelf narrower anteriorly.



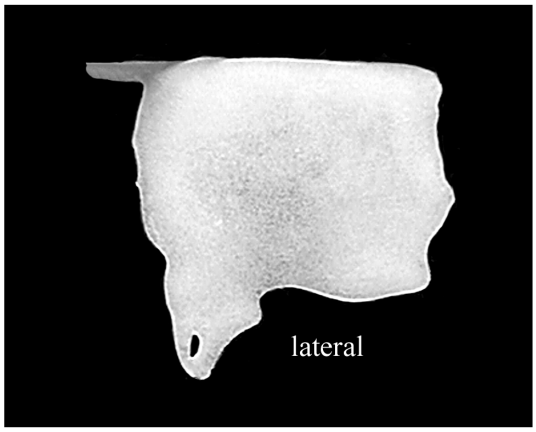
96(1): CJB 715, *contortrix* (rt. nasal, dorsal); dorsal shelf narrower posteriorly.



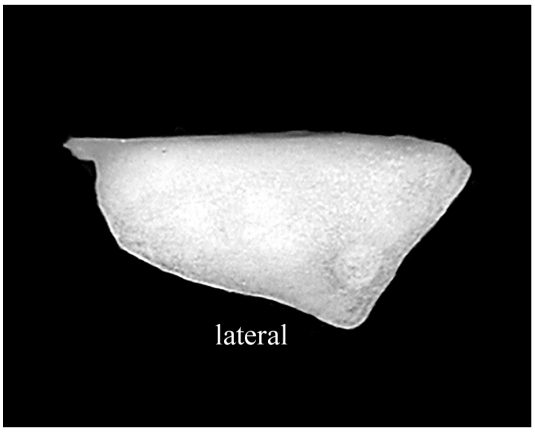
97(0): CJB 715, *contortrix* (rt. nasal, dorsal); dorsal shelf longer than wide.



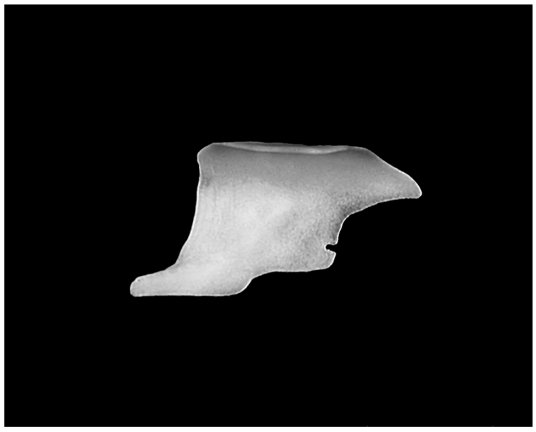
97(1): CJB 650, *cerastes* (rt. nasal, dorsal); dorsal shelf wider than long.



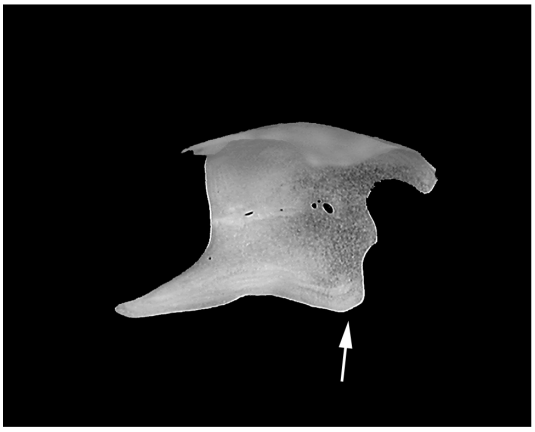
98(0): CJB 490, *ruber* (rt. nasal, dorsal); lateral margin emarginated or with projection(s).



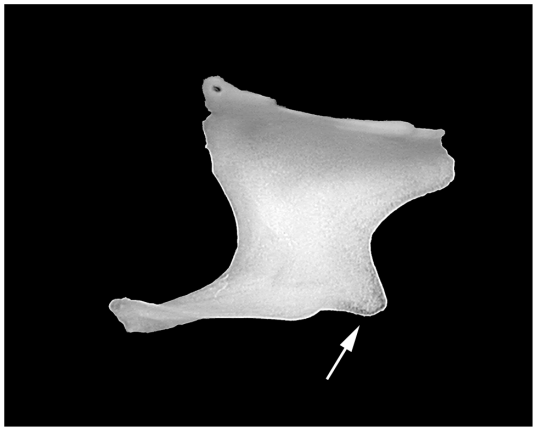
98(1): CJB 715, *contortrix* (rt. nasal, dorsal); lateral margin smooth, no projection(s) or emargination.



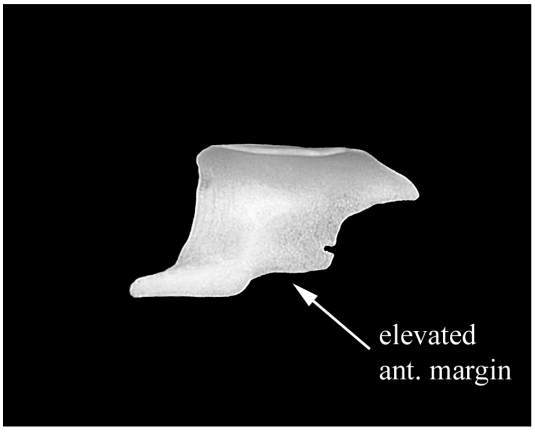
99(0): CJB 508, *piscivorus* (rt. nasal, lateral); no anterior projection from ventral edge of median shelf.



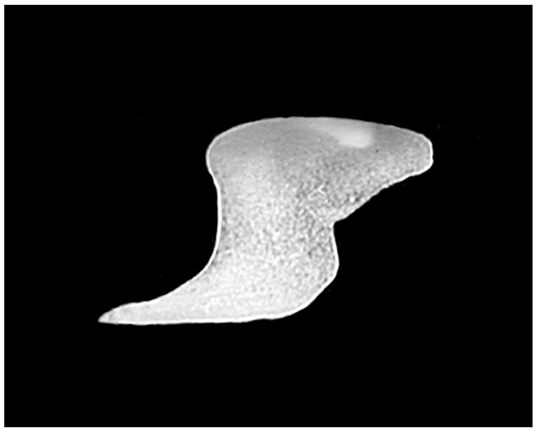
99(1): CJB 577, *atrox* (rt. nasal, lateral); small anterior projection (bump) from ventral edge of median shelf.



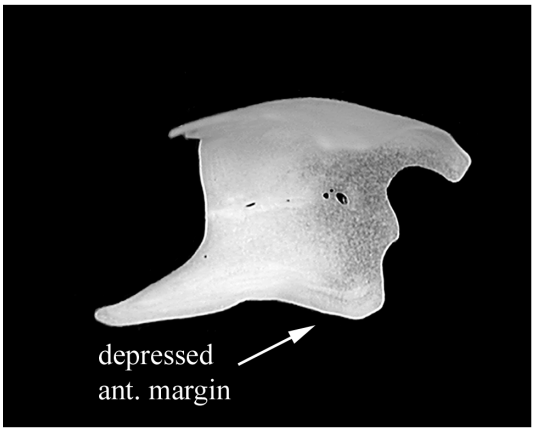
99(2): CJB 490, *ruber* (rt. nasal, lateral); large anterior projection from ventral edge of median shelf.



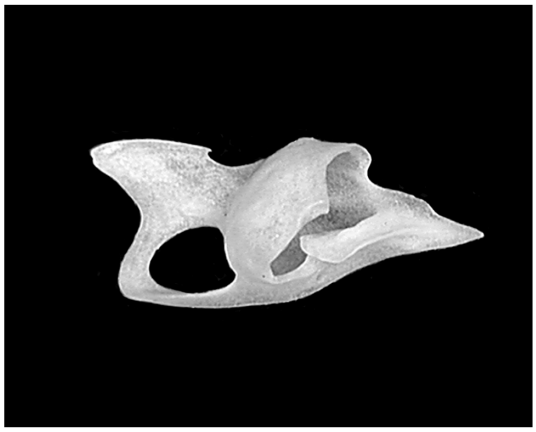
100(0): CJB 508, *piscivorus* (rt. nasal, lateral); entire ventral edge not in same horizontal plane, anterior portion slightly elevated/dorsal.



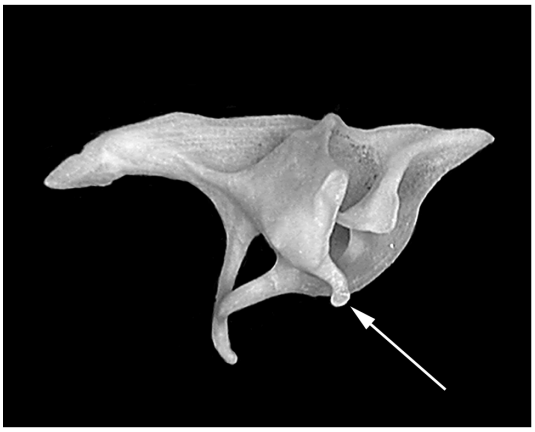
100(1): CJB 690, *miliarius* (rt. nasal, lateral); entire ventral edge in same horizontal plane.



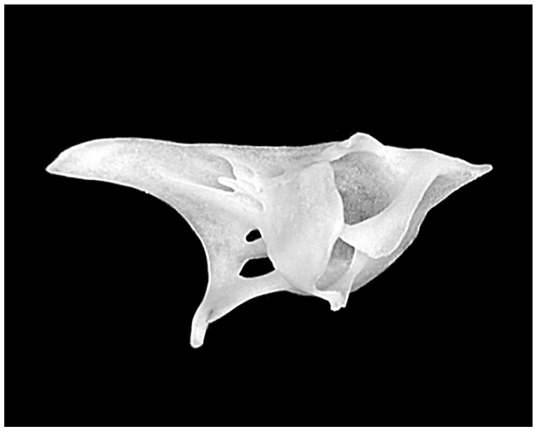
100(2): CJB 577, *atrox* (rt. nasal, lateral); entire ventral edge not in same horizontal plane, anterior portion slightly depressed/ventral.



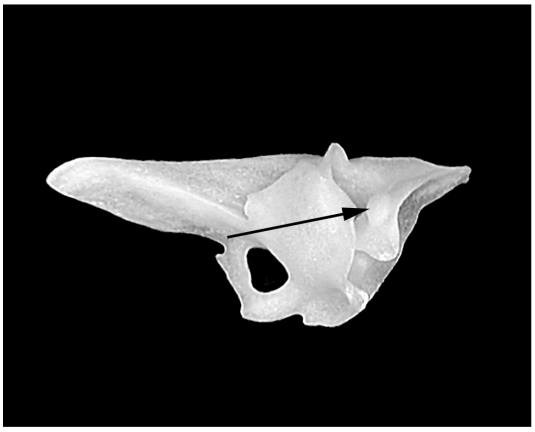
101(0): CJB 715, *contortrix* (rt. vomer, lateral); small pointed ventral process absent from margin of fenestra vomeronasal externa.



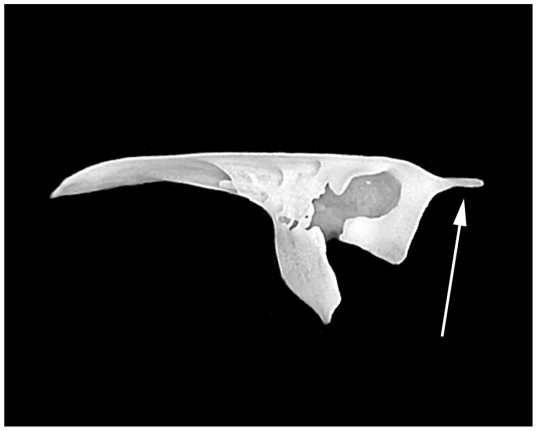
101(1): CJB 573, *atrox* (rt. vomer, lateral); small pointed ventral process present on margin of fenestra vomeronasal externa.



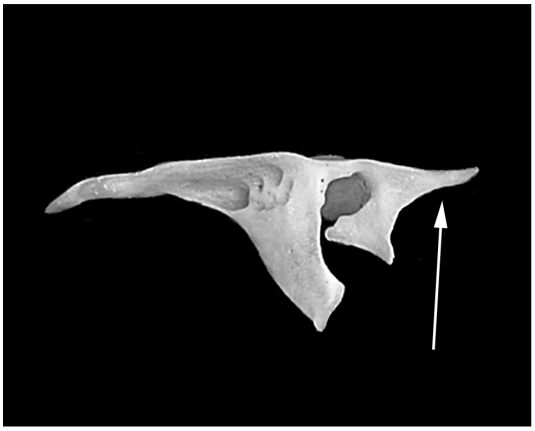
102(0): CJB 001, *atrox* (rt. vomer, lateral); process on inner margin of fenestra vomeronasal externa absent.



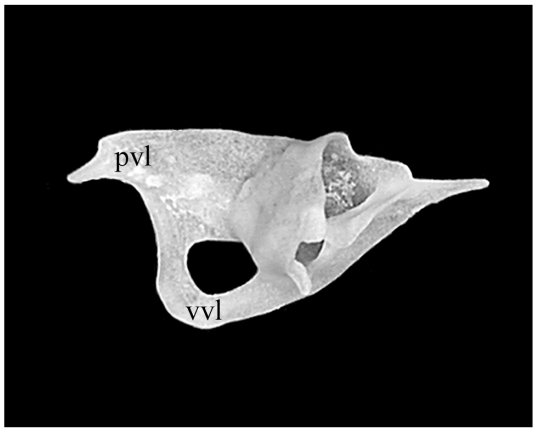
102(1): NAUQSP 14086, *basiliscus* (rt. vomer, lateral); process on inner margin of fenestra vomeronasal externa present.



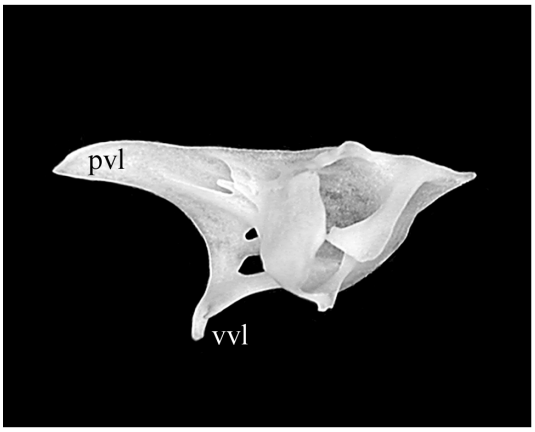
103(0): CJB 001, *atrox* (rt. vomer, dorsal); anterodorsal process is thin, finger-like narrow process.



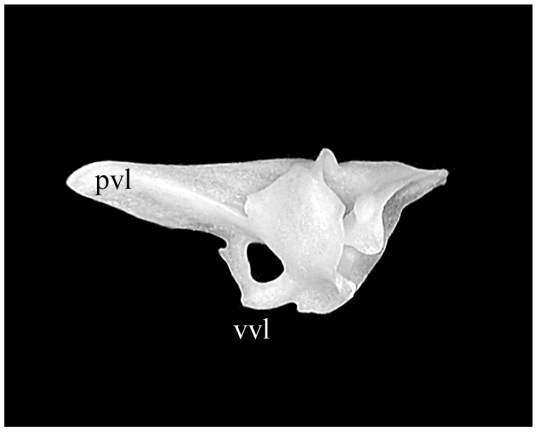
103(0): CJB 573, *atrox* (rt. vomer, dorsal); anterodorsal process is triangular, not finger-like narrow process.



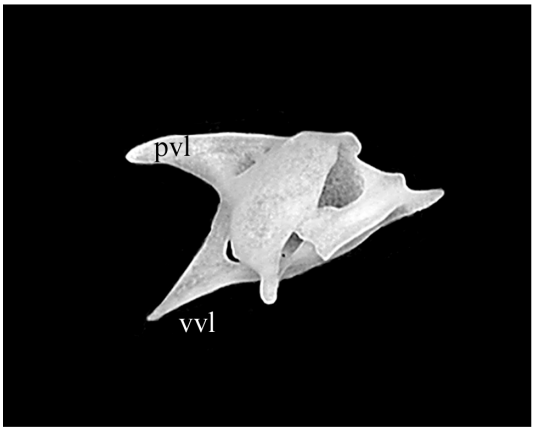
104(0): CJB 685, *piscivorus* (rt. vomer, lateral); posterior and ventral vertical laminae share large portion of vertical shelf.



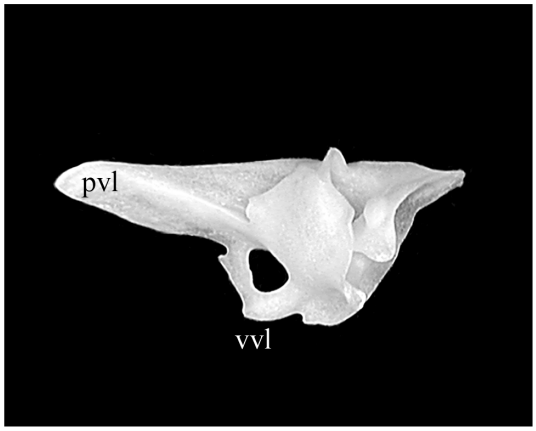
104(1): CJB 001, *atrox* (rt. vomer, lateral); posterior and ventral vertical laminae do not share large portion of vertical shelf.



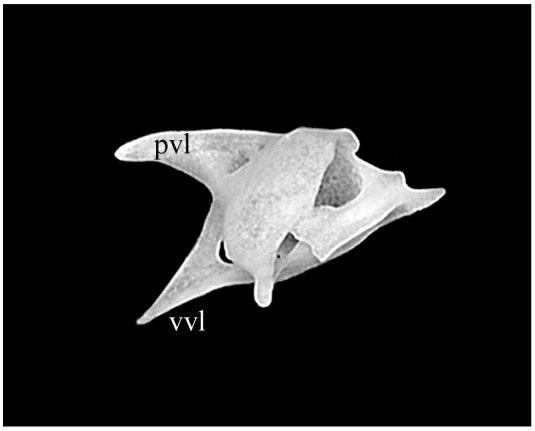
105(0): NAUQSP 14086, *basiliscus* (rt. vomer, lateral); posterior tip of posterior laminae extends further caudally.



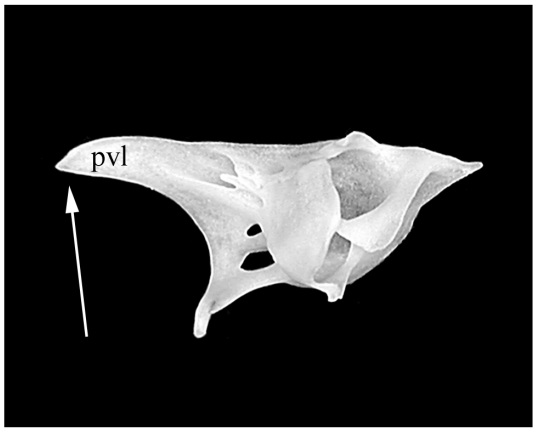
105(1): CJB 691, *catenatus* (rt. vomer, lateral); posterior tips of both posterior and vertical laminae equidistant caudally.



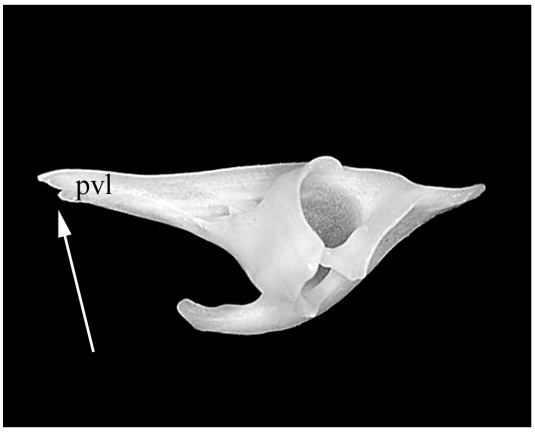
106(0): NAUQSP 14086, *basiliscus* (rt. vomer, lateral); margin between posterior and vertical laminae not U-shaped.



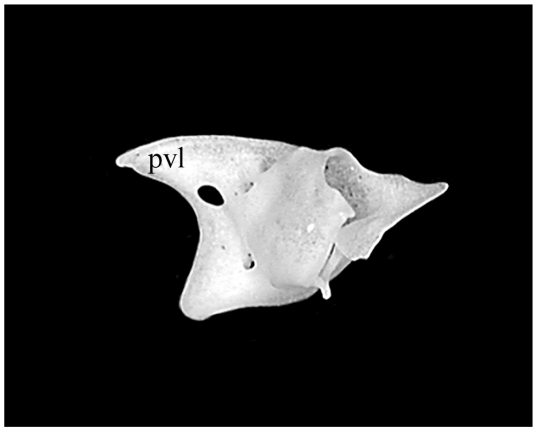
106(1): CJB 691, *catenatus* (rt. vomer, lateral); margin between posterior and vertical laminae U-shaped.



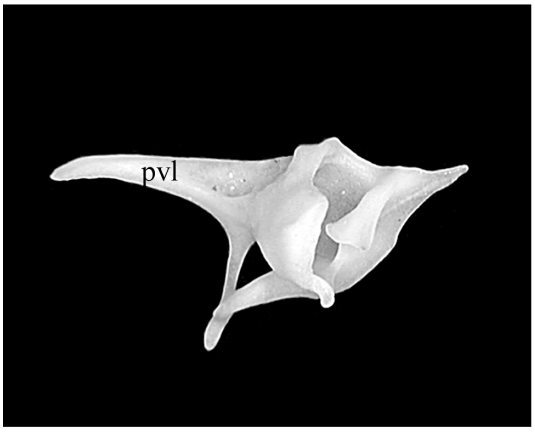
107(0): CJB 001, *atrox* (rt. vomer, lateral); distal end of posterior vertical lamina entire, not notched or forked.



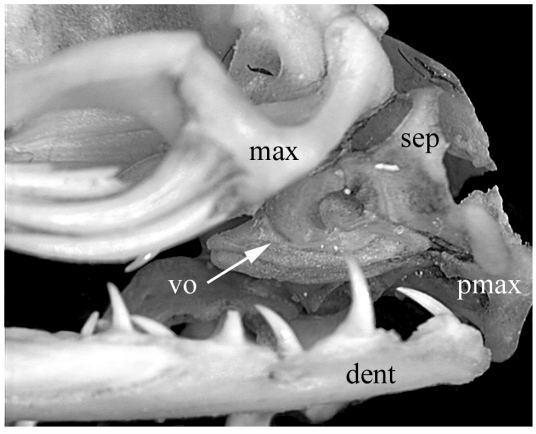
107(1): CJB 1064, *enyo* (rt. vomer, lateral); distal end of posterior vertical lamina notched or forked.



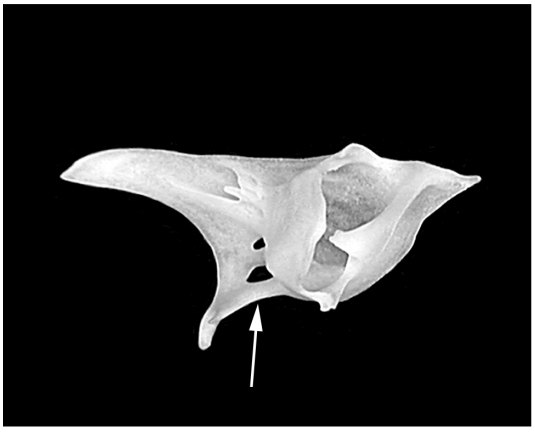
108(0): CJB 699, *cerastes* (rt. vomer, lateral); posterior vertical lamina length less than height of vomer.



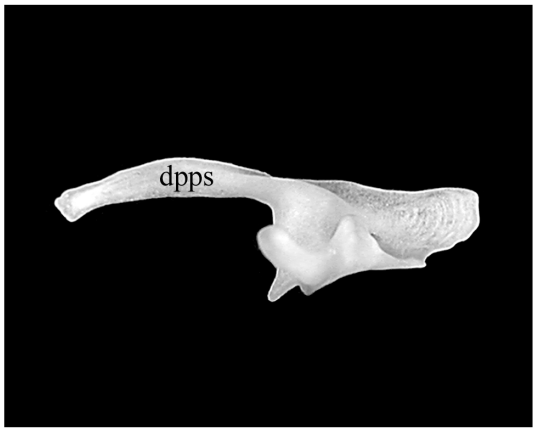
108(1): CJB 577, *atrox* (rt. vomer, lateral); posterior vertical lamina length greater than or equal to height of vomer.



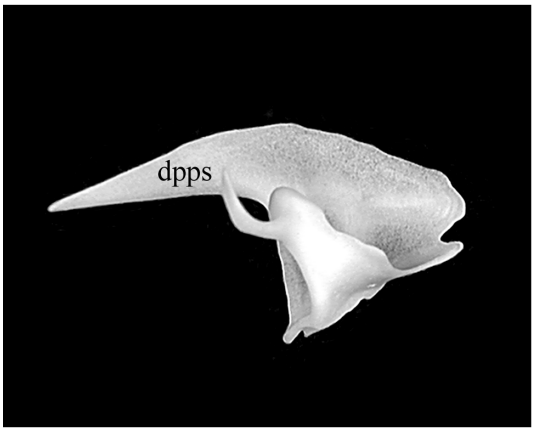
109(0): LSUMZ 35365, *pricei* (rt. side of skull, lateral); ventral vertical lamina foramen absent.



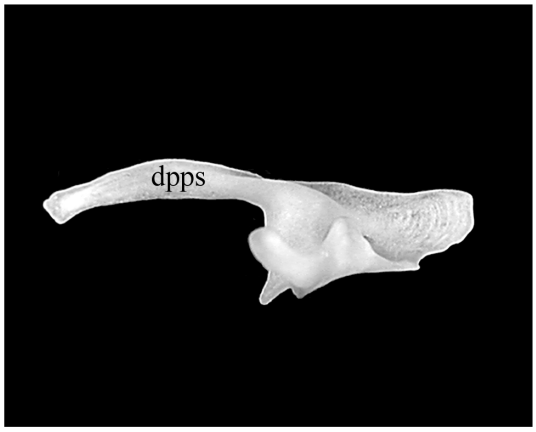
109(1): CJB 001, *atrox* (rt. vomer, lateral); ventral vertical lamina foramen (or foramina) present.



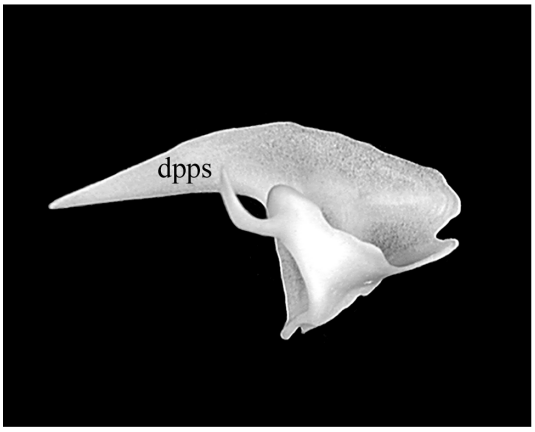
110(0): CJB 692, *bilineatus* (rt. septomaxilla, lateral); dorsoposterior process constricted at proximal connection with rest of bone.



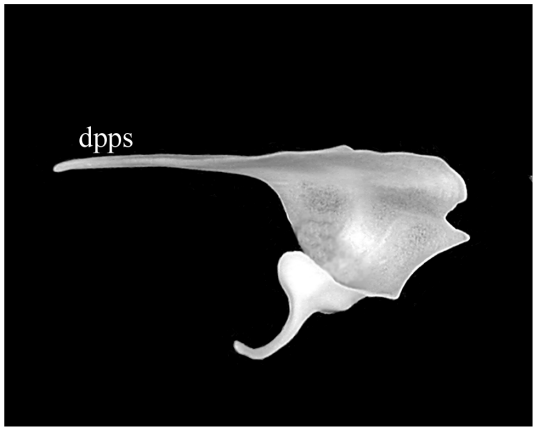
110(1): CJB 001, *atrox* (rt. septomaxilla, lateral); dorsoposterior process not constricted at proximal connection with rest of bone.



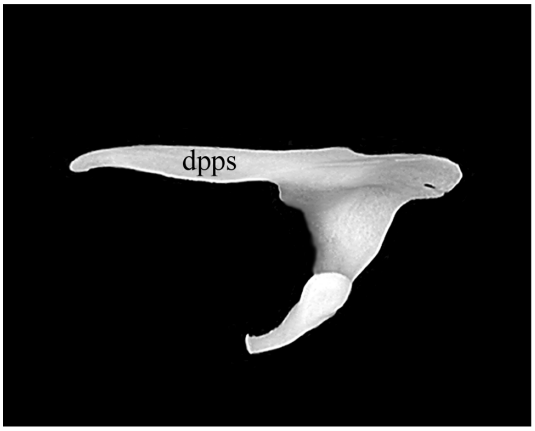
111(0): CJB 692, *bilineatus* (rt. septomaxilla, lateral); dorsoposterior process terminates as rounded lamina.



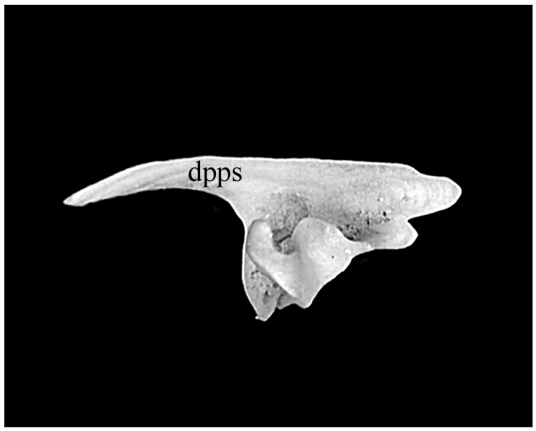
111(1): CJB 001, *atrox* (rt. septomaxilla, lateral); dorsoposterior process tapers into narrow and pointed lamina.



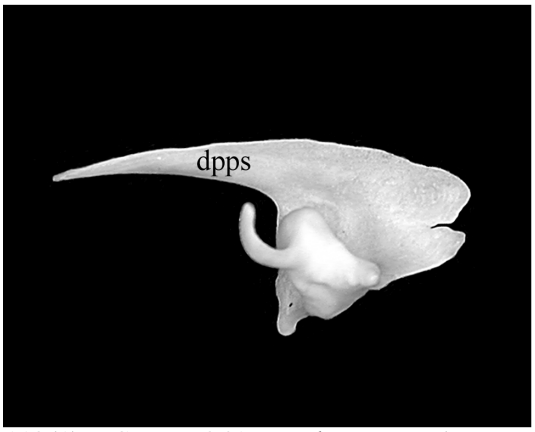
112(0): CJB 001, *atrox* (rt. septomaxilla, dorsal); narrow, pointed lamina of dorsoposterior process in vertical orientation.



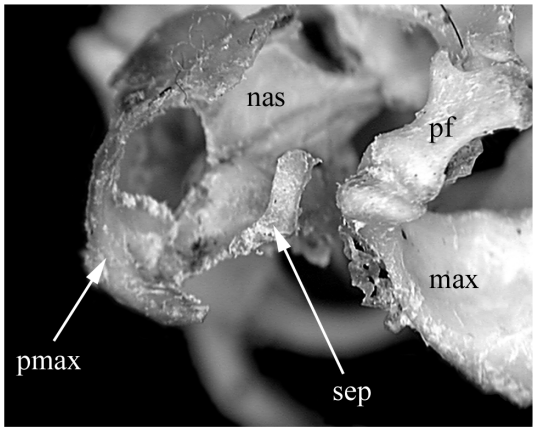
112(1): LSUMZ 10340, *horridus* (rt. septomaxilla, dorsal); narrow, pointed lamina of dorsoposterior process in vertical orientation.



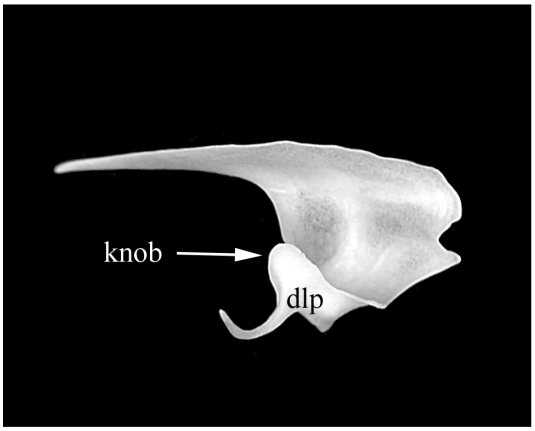
113(0): TJL 930, *polystictus* (rt. septomaxilla, lateral); dorsoposterior process shorter than body of septomaxilla.



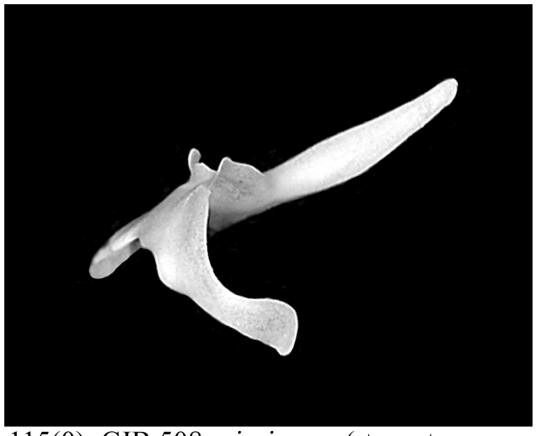
113(1): LSUMZ 34177, *adamanteus* (rt. septomaxilla, lateral); dorsoposterior process longer than or equal to body of septomaxilla.



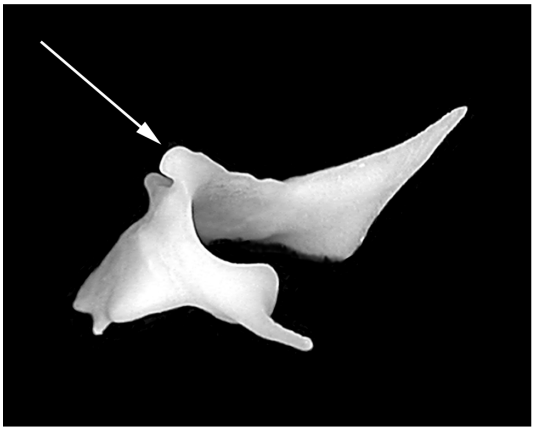
114(0): FMNH 73969, *blomhoffii* (left skull, lateral); dorsolateral process with rounded edges and without thickened medial knob.



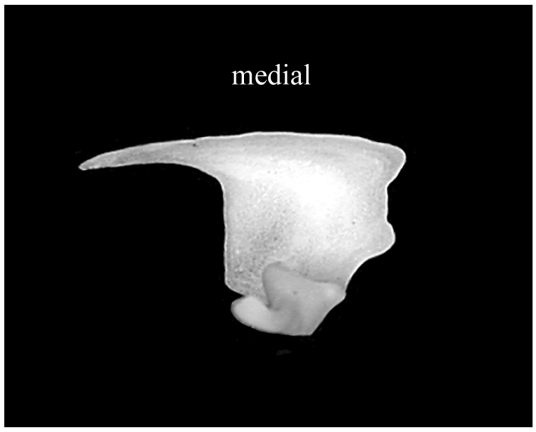
114(1): CJB 001, *atrox* (rt. septomaxilla, lateral); dorsolateral process with thickened medial knob.



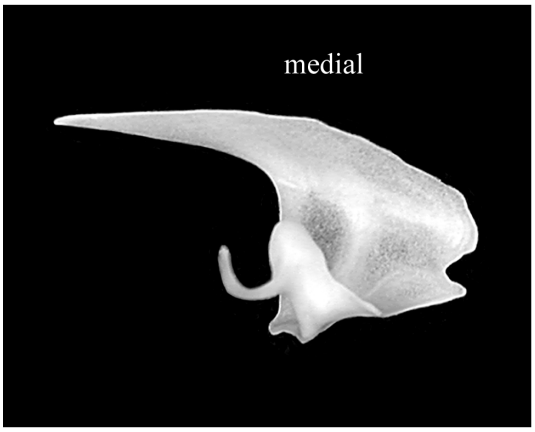
115(0): CJB 508, *piscivorus* (rt. septomaxilla, ventrolateral); absence of distinct projection along posterolateral margin.



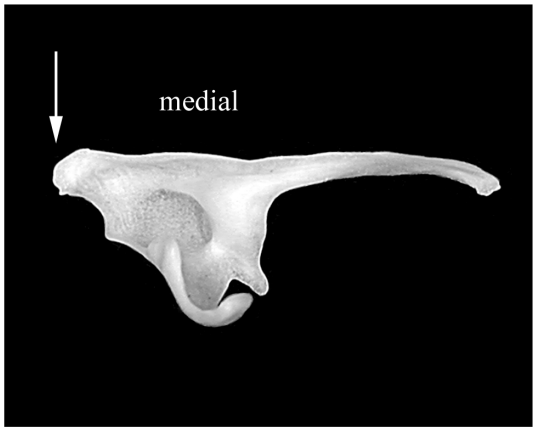
115(1): CJB 490, *ruber* (rt. septomaxilla, ventrolateral); presence of distinct projection along posterolateral margin.



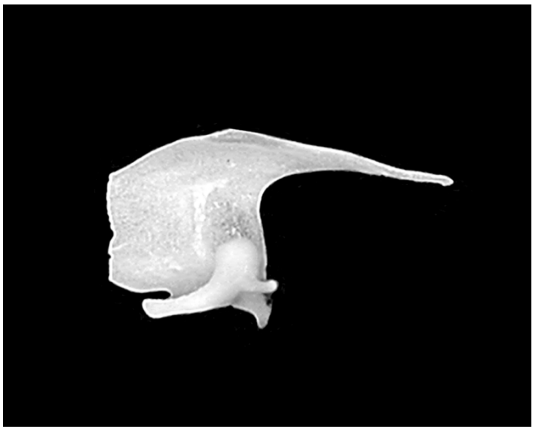
116(0): CJB 699, *cerastes* (rt. septomaxilla, lateral); anteromedial corner of bone in same horizontal plane as rest of dorsal edge.



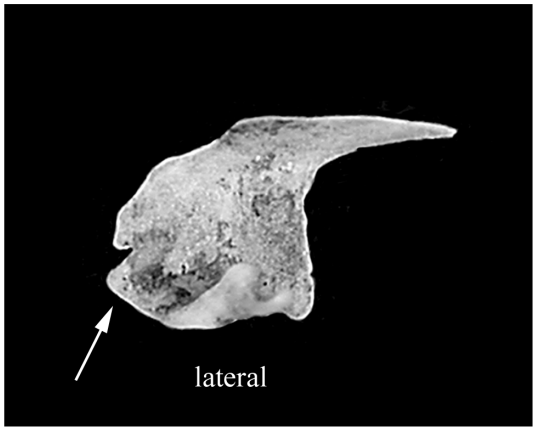
116(1): CJB 001, *atrox* (rt. septomaxilla, lateral); anteromedial corner of bone not in same horizontal plane as rest of dorsal edge.



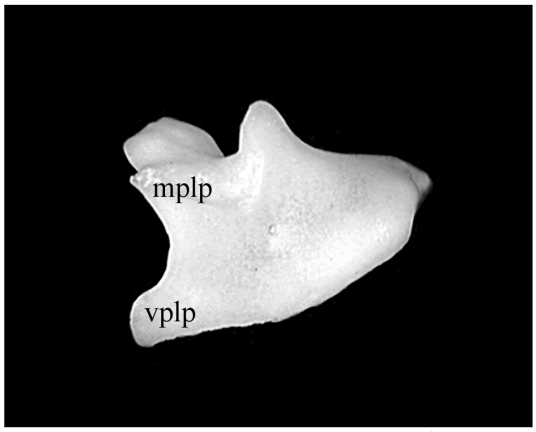
117(0): CJB 692, *bilineatus* (left septomaxilla, lateral); medial portion of anterior margin extends further anteriorly than rest of margin.



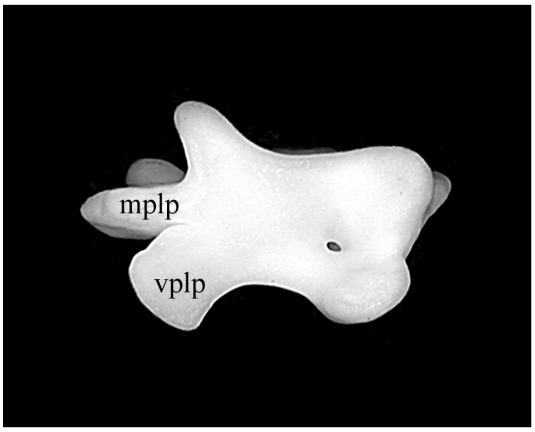
117(1): CM 145603, *ruber* (left septomaxilla, lateral); both lateral and medial portions of anterior margin extend equal distance anteriorly.



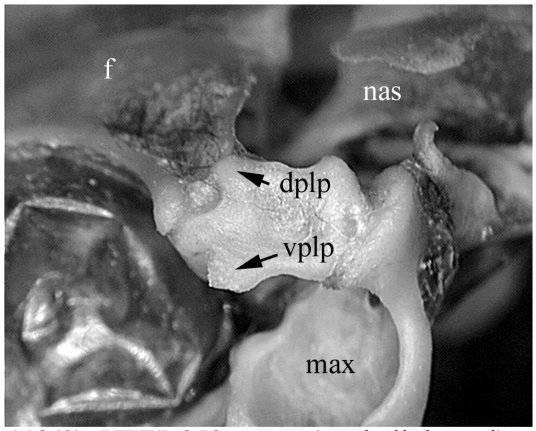
117(2): SDNHM 46949, *catalinensis* (left septomaxilla, lateral); lateral portion of anterior margin extends further anteriorly than rest of margin.



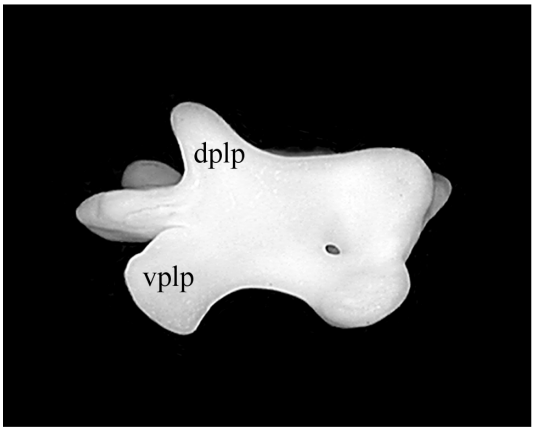
118(0): CJB 508, *piscivorus* (rt. prefrontal, lateral); middle and ventral posterolateral processes equal in length.



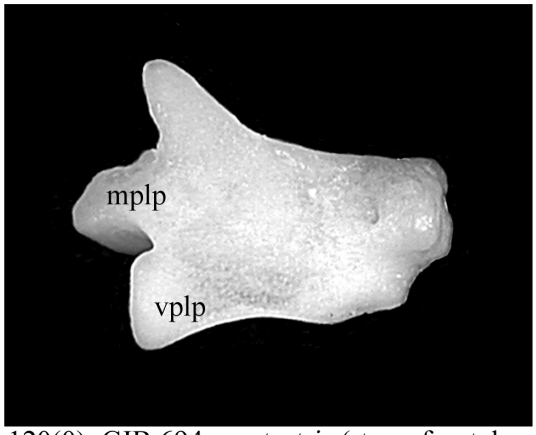
118(1): CJB 001, *atrox* (rt. prefrontal, lateral); middle posterolateral process longer than ventral posterolateral process.



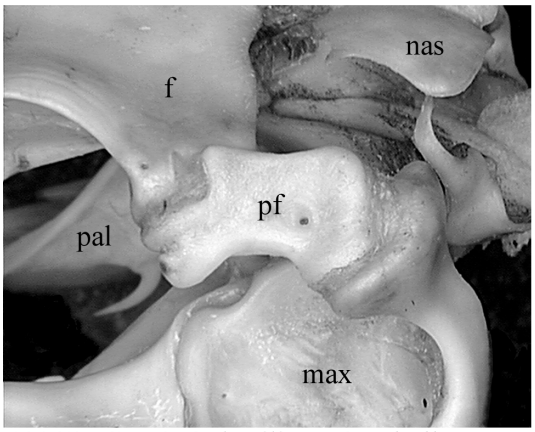
119(0): UTEP 959, *ravus* (rt. skull, lateral); dorsal and ventral posterolateral processes extend equal lengths caudally.



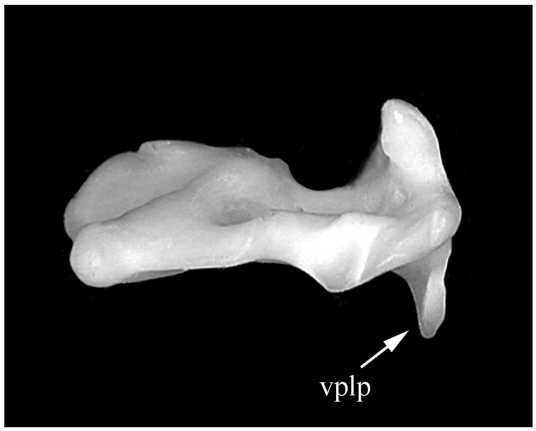
119(1): CJB 001, *atrox* (rt. prefrontal, lateral); ventral posterolateral process extends further caudally than dorsal process.



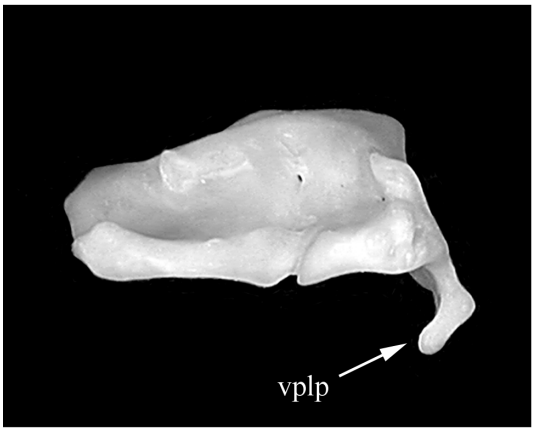
120(0): CJB 694, *contortrix* (rt. prefrontal, lateral); middle and ventral posterolateral processes not fused.



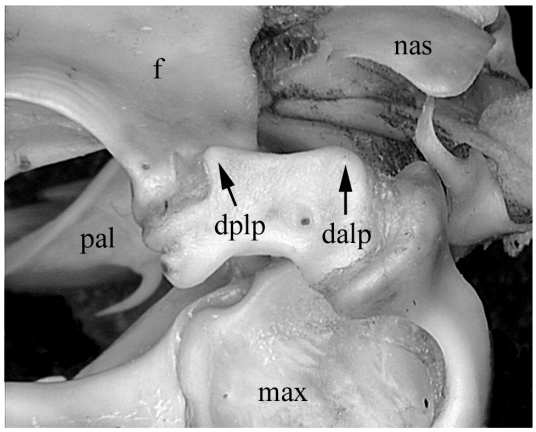
120(1): CJB 258, *basiliscus* (rt. skull, lateral); middle and ventral posterolateral processes fused.



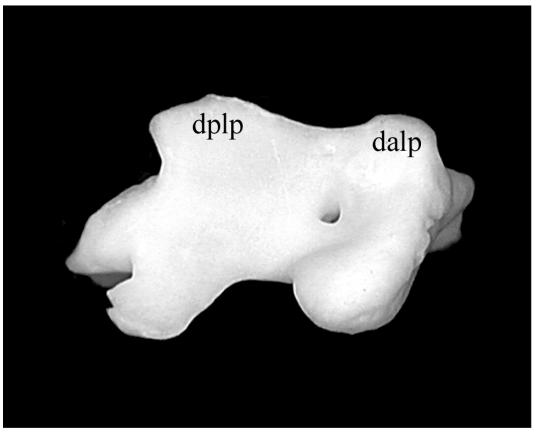
121(0): CJB 001, *atrox* (rt. prefrontal, posterior); ventral posterolateral process without medial projection.



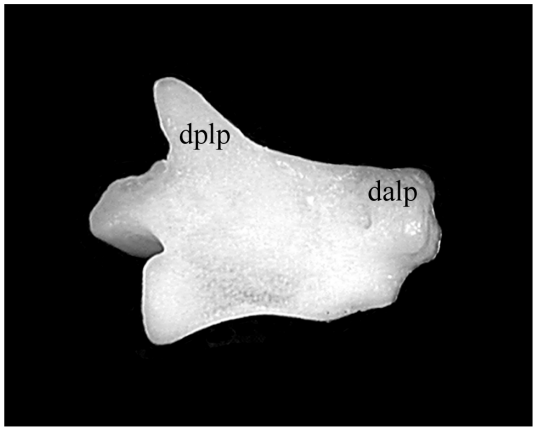
121(1): CJB 692, *bilineatus* (rt. prefrontal, posterior); ventral posterolateral process with medial projection.



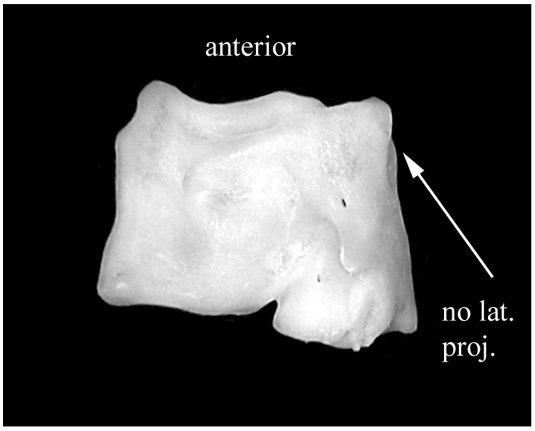
122(0): CJB 258, *basiliscus* (rt. skull, lateral); dorsal posterolateral process same height as dorsal anterolateral process.



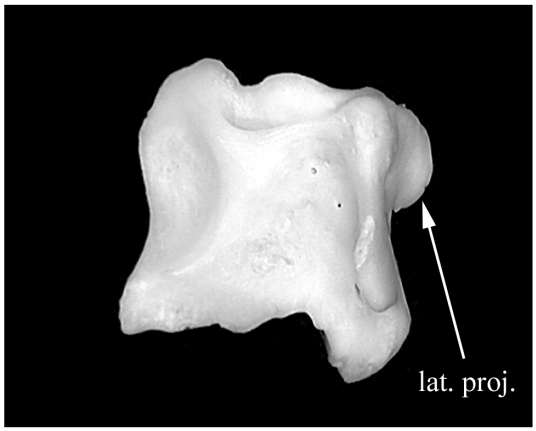
122(1): CJB 490, *ruber* (rt. prefrontal, lateral); dorsal posterolateral process slightly higher than dorsal anterolateral process.



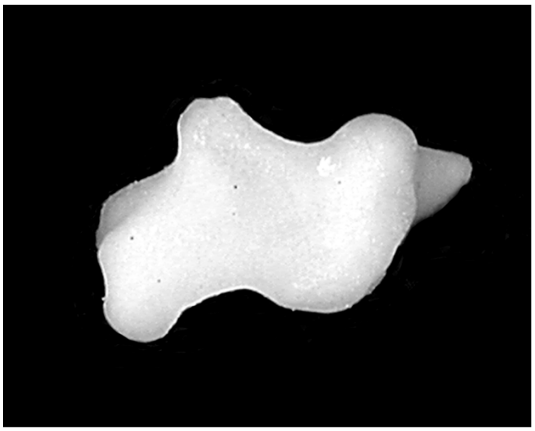
122(2): CJB 694, *contortrix* (rt. prefrontal, lateral); dorsal posterolateral process twice as high as dorsal anterolateral process.



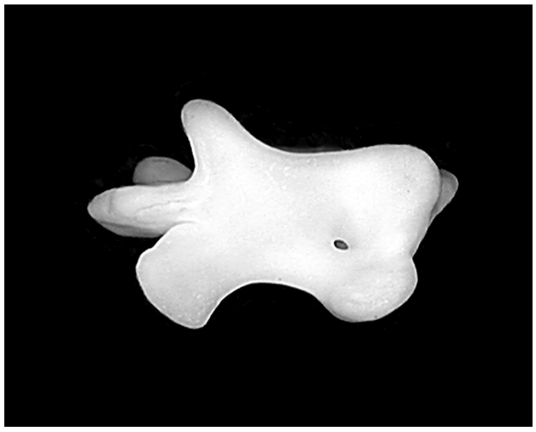
123(0): CJB 692, *bilineatus* (rt. prefrontal, dorsal); lateral or ventral projection absent on ventral anterolateral surface.



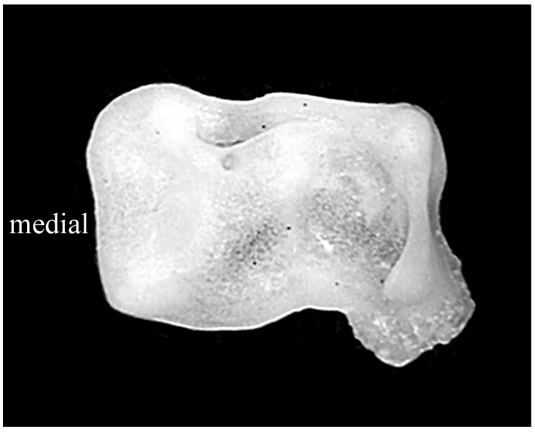
123(1): CJB 490, *ruber* (rt. prefrontal, dorsal); lateral or ventral projection present on ventral anterolateral surface.



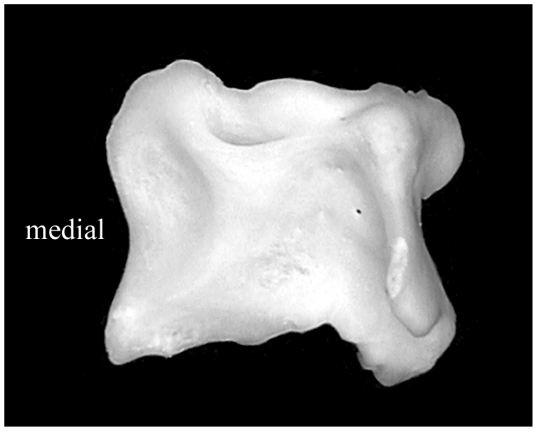
124(0): CJB 699, *cerastes* (rt. prefrontal, lateral); foramen absent in anterolateral wall.



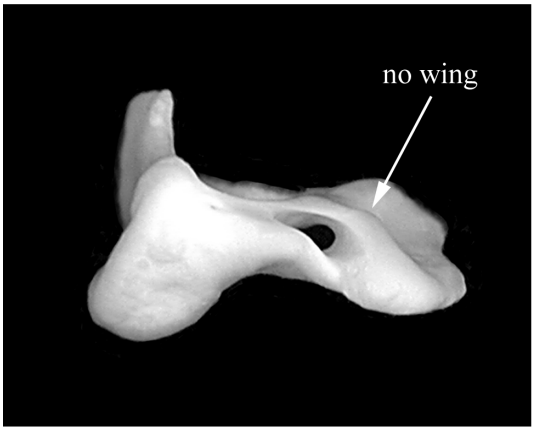
124(1): CJB 001, *atrox* (rt. prefrontal, lateral); foramen present in anterolateral wall.



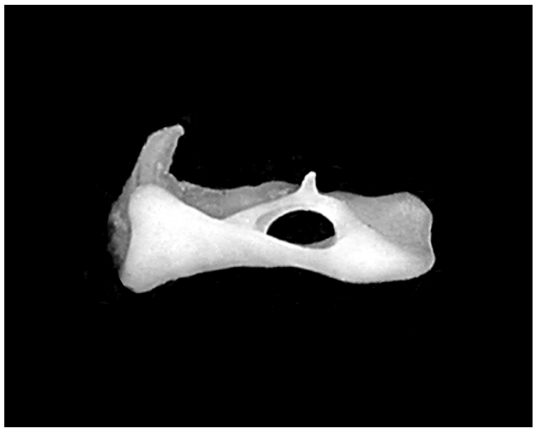
125(0): CJB 1060, *lepidus* (rt. prefrontal, dorsal); medial margin not concave.



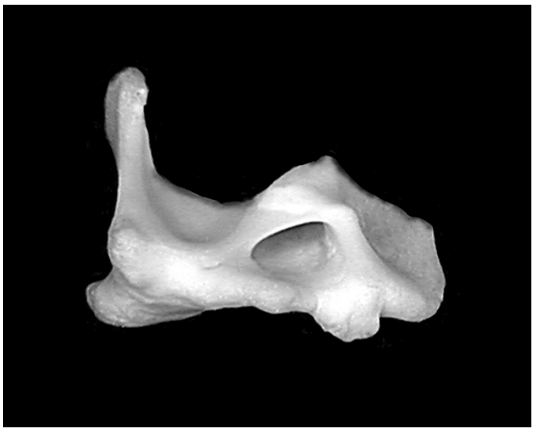
125(1): CJB 490, *ruber* (rt. prefrontal, dorsal); medial margin concave.



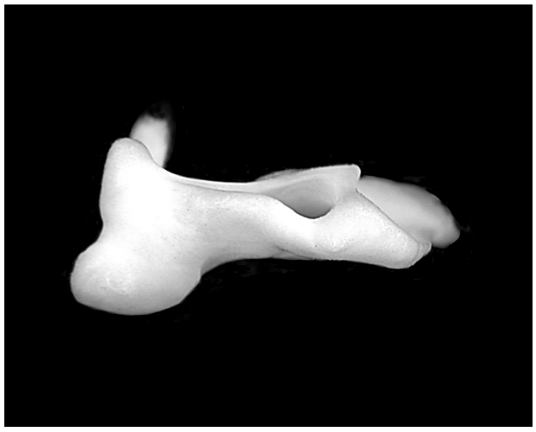
126(0): CJB 1060, *lepidus* (rt. prefrontal, anterior); anteromedial wing absent.



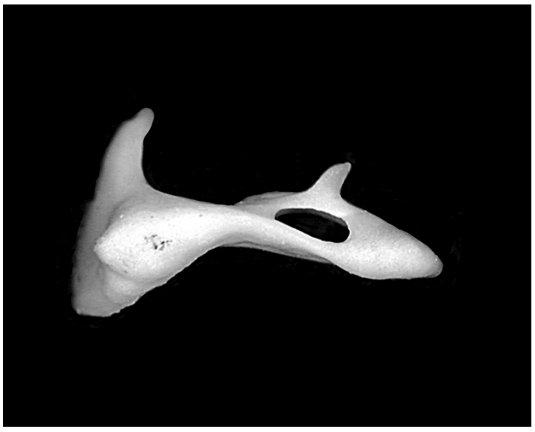
126(1): CJB 490, *ruber* (rt. prefrontal, anterior); anteromedial wing present.



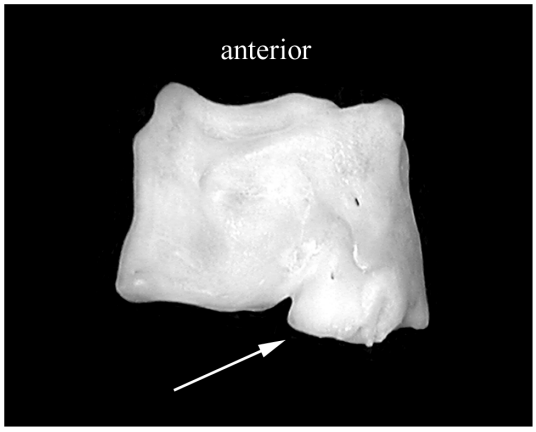
127(0): CJB 574, *atrox* (rt. prefrontal, anterior); anteromedial wing only low bump.



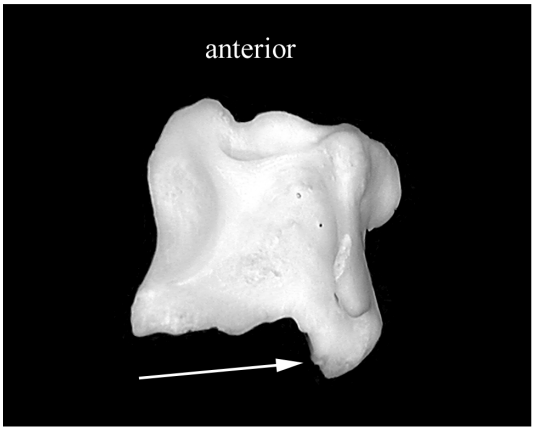
127(1): CJB 001, *atrox* (rt. prefrontal, anterior); anteromedial wing formed by raised anterior margin.



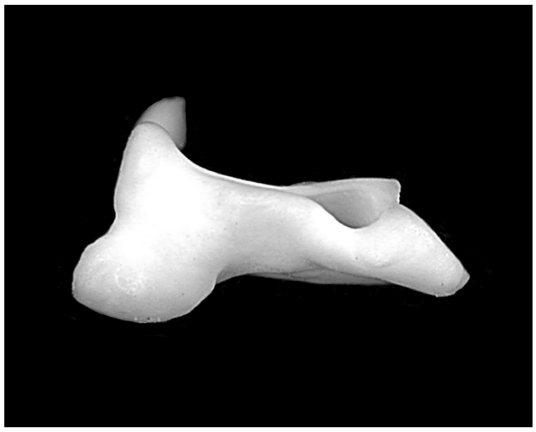
127(2): CJB 715, *contortrix* (rt. prefrontal, anterior); anteromedial wing formed by distinct raised process.



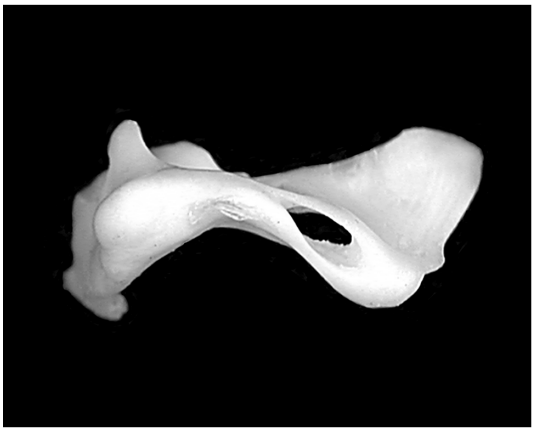
128(0): CJB 692, *bilineatus* (rt. prefrontal, dorsal); posterior margin mostly straight, with slight posterior bulge posterolaterally.



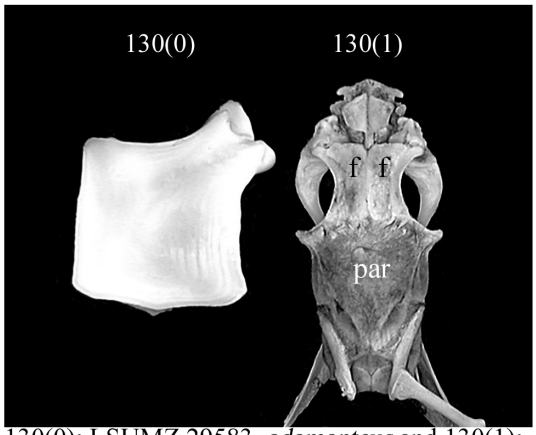
128(1): CJB 490, *ruber* (rt. prefrontal, dorsal); only 2/3 posterior margin straight, with large posterior bulge posterolaterally.



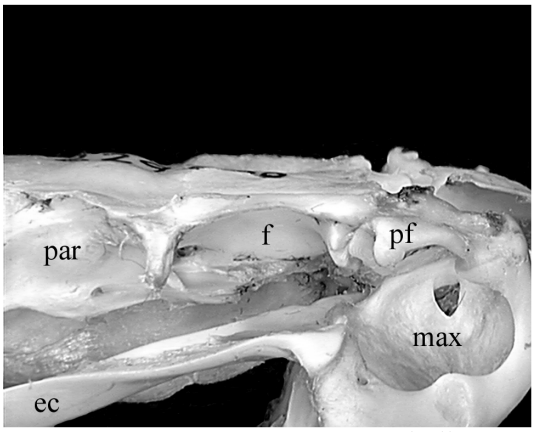
129(0): CJB 001, *atrox* (rt. prefrontal, anterior); entire bone not bent in horizontal plane.



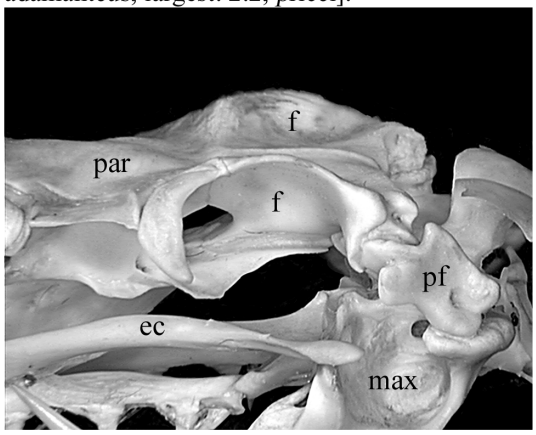
129(1): CJB 508, *piscivorus* (rt. prefrontal, anterior); entire bone bent in horizontal plane.



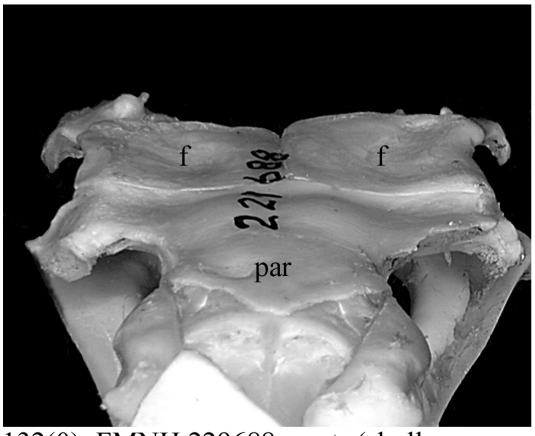
130(0): LSUMZ 29583, *adamanteus* and 130(1): LSUMZ 35365, *pricei* (frontal and skull, dorsal); frontal shape, length/width ratio [smallest: 0.9, *adamanteus*; largest: 2.2, *pricei*].



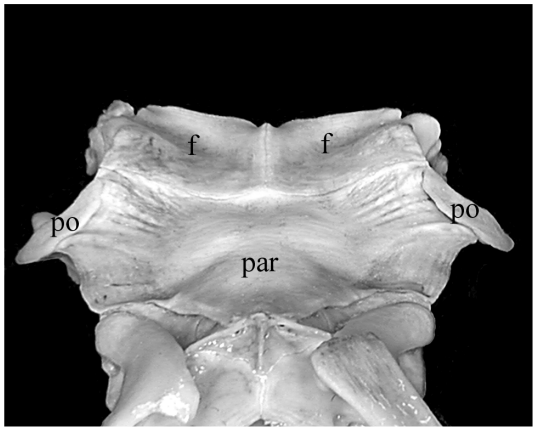
131(0): FMNH 229688, *muta* (rt. skull, lateral); lateral frontal margin flat.



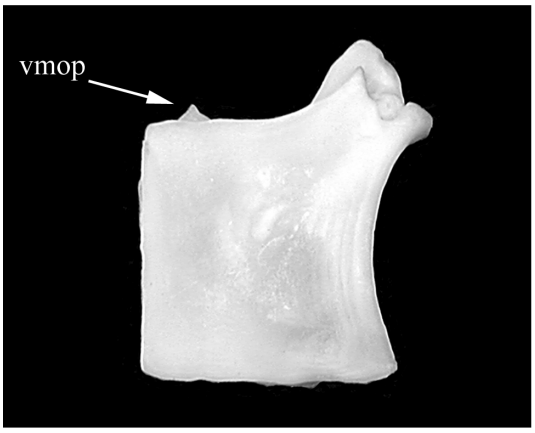
131(1): TJL 950, *atrox* (rt. skull, lateral); lateral frontal margin elevated.



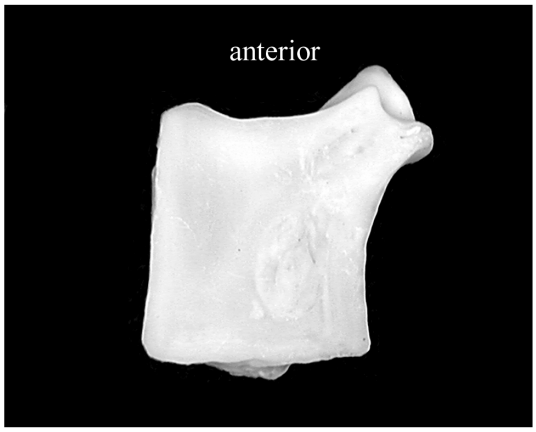
132(0): FMNH 229688, *muta* (skull, lateral); anterior frontal margin flat.



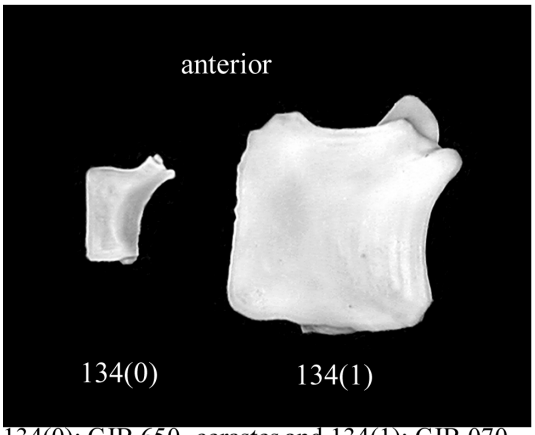
132(1): TJL 950, *atrox* (skull, lateral); anterior frontal margin elevated.



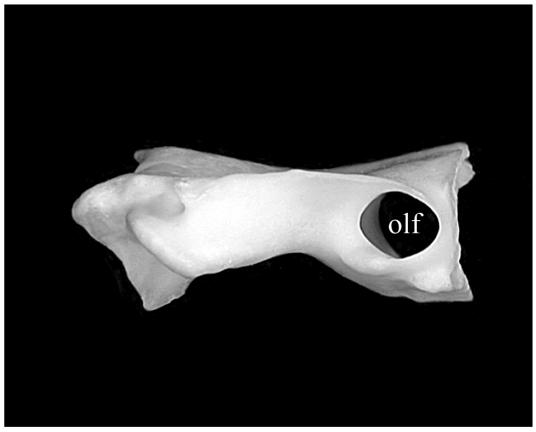
133(0): CJB 001, *atrox* (rt. frontal, dorsal); medial half of anterior margin not concave (note ventral margin of olfactory foramen).



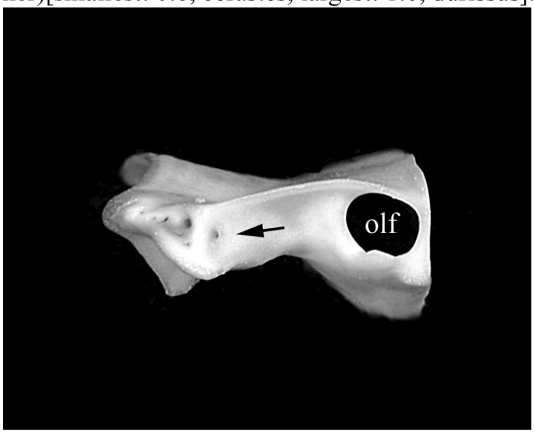
133(1): CJB 577, *atrox* (rt. frontal, dorsal); medial half of anterior margin concave.



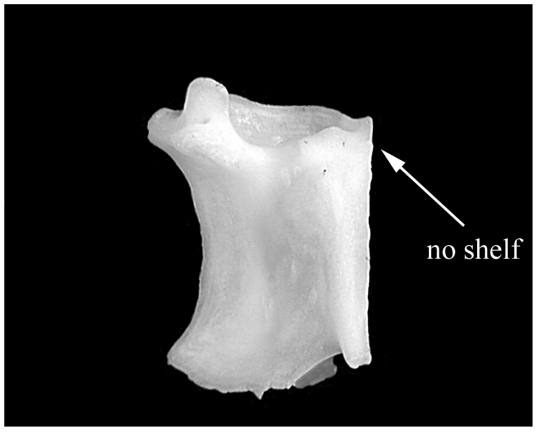
134(0): CJB 650, *cerastes* and 134(1): CJB 070, *durissus* (rt. frontal, dorsal); ratio posterior width (to lateral corner)/anerior width (to anterior corner)[smallest: 0.6, *cerastes;* largest: 1.0, *durissus*].



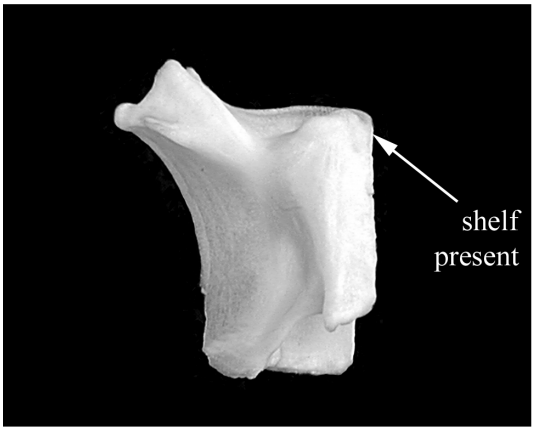
135(0): CJB 001, *atrox* (rt. frontal, anterior); absence of small foramina lateral to olfactory foramen.



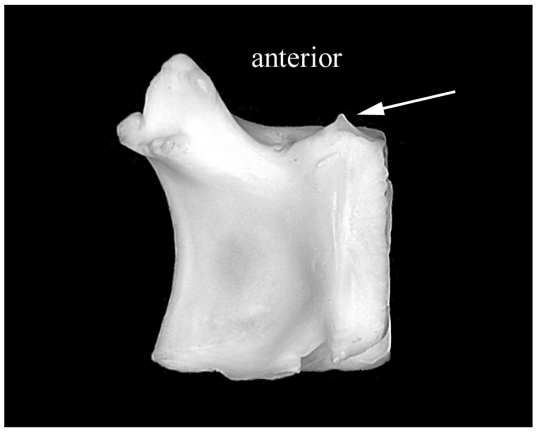
135(1): LSUMZ 21210, *ruber* (rt. frontal, anterior); presence of small foramina lateral to olfactory foramen.



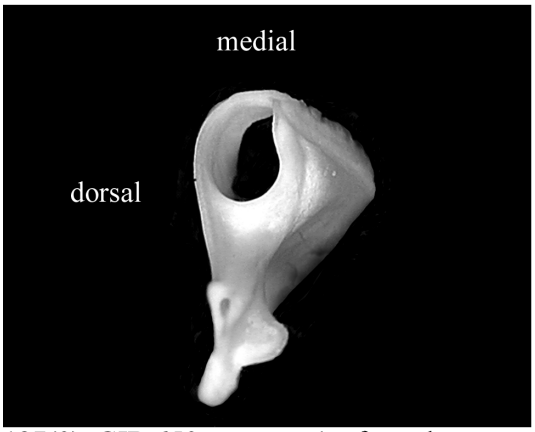
136(0): CJB 1062, *pricei* (rt. frontal, ventral); no shelf present along ventral margin of olfactory foramen.



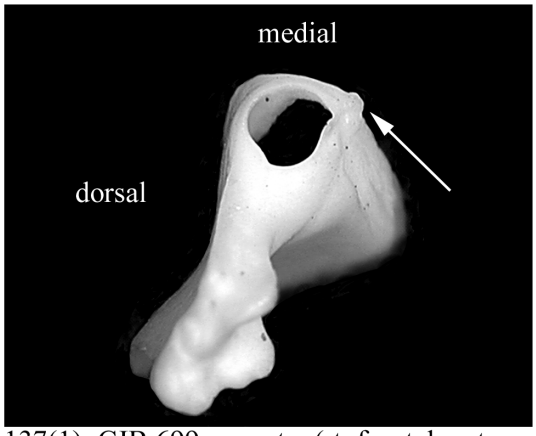
136(1): CJB 650, *cerastes* (rt. frontal, ventral); horizontal shelf present, projecting anteriorly less than anterodorsal margin of frontal.



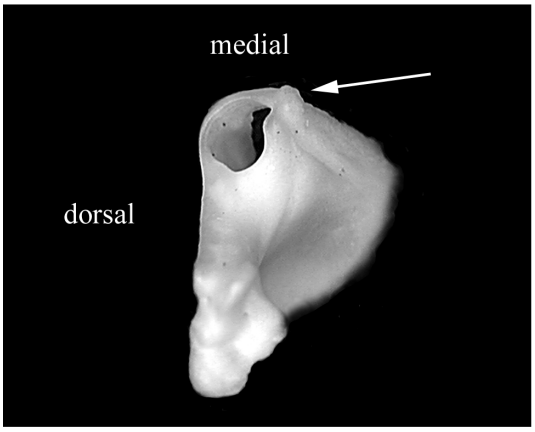
136(2): CJB 001, *atrox* (rt. frontal, ventral); horizontal shelf present, projecting further anteriorly than anterodorsal margin of frontal.



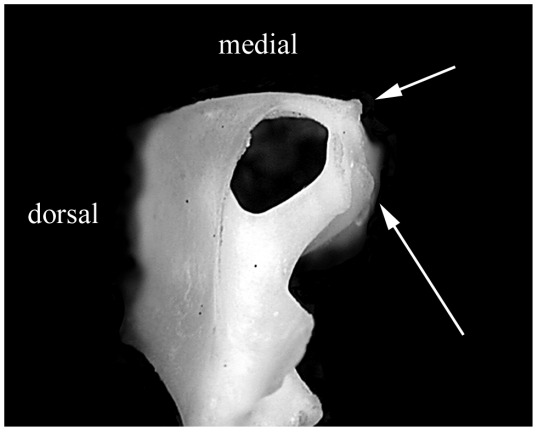
137(0): CJB 650, *cerastes* (rt. frontal, anteroventral); distinct vomerine process absent below olfactory foramen.



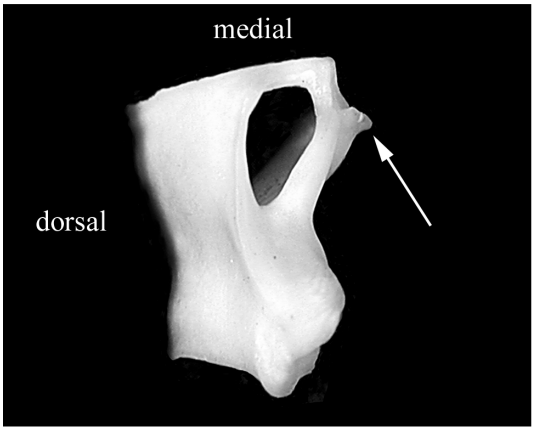
137(1): CJB 699, *cerastes* (rt. frontal, anteroventral); distinct vomerine process present below olfactory foramen.



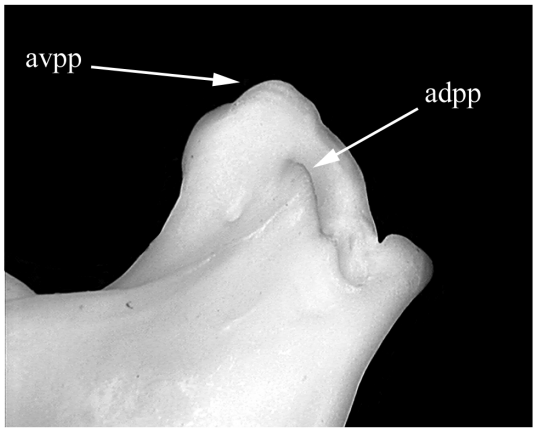
138(0): CJB 699, *cerastes* (rt. frontal, anteroventral); vomerine process of frontal medial to olfactory foramen.



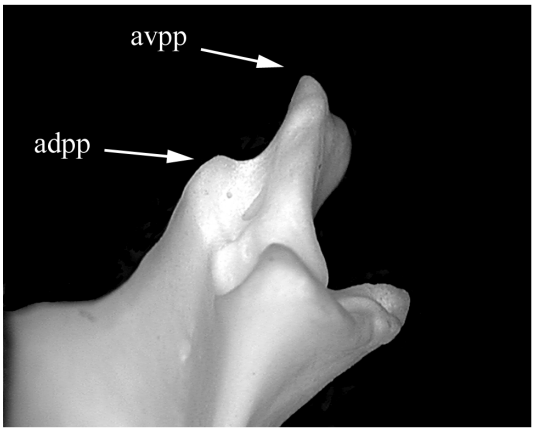
138(1): CJB 1062, *lepidus* (rt. frontal, anterodorsal); vomerine processes of frontal present both medial and lateral to olfactory foramen.



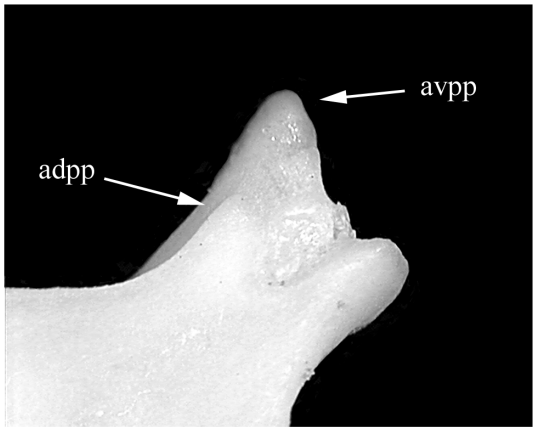
138(2): CJB 715, *contortrix* (rt. frontal, anterodorsal); vomerine process of frontal lateral to olfactory foramen.



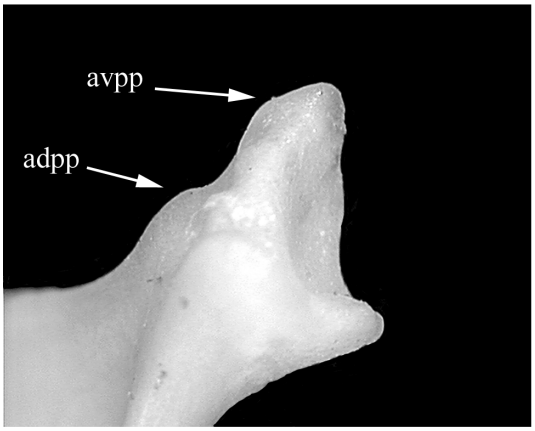
139(0): CJB 001, *atrox* (rt. frontal, dorsal); anterodorsal prefrontal process distinct from and extending over anteroventral process.



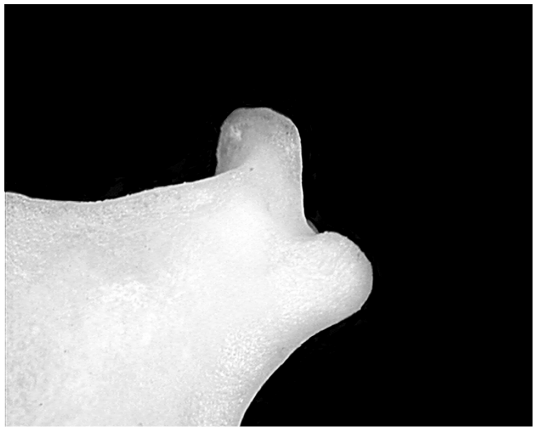
139(0): CJB 001, *atrox* (rt. frontal, lateral); anterodorsal prefrontal process distinct from and extending over anteroventral process.



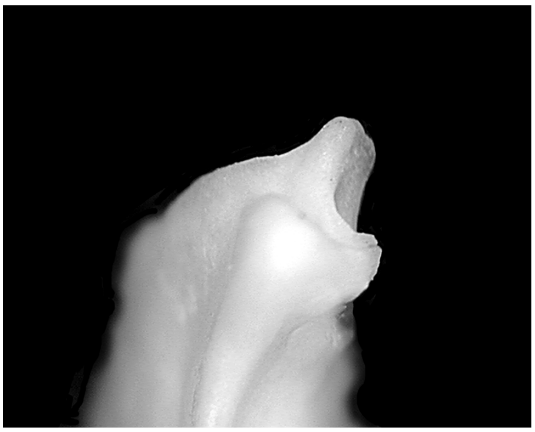
139(1): CJB 694, *contortrix* (rt. frontal, dorsal); anterodorsal prefrontal process distinct from, but not extending over, anteroventral process.



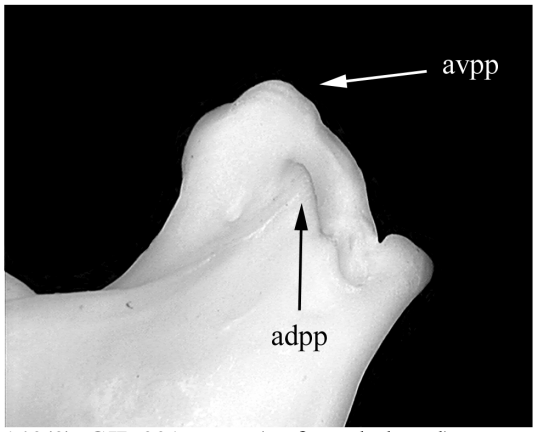
139(1): CJB 694, *contortrix* (rt. frontal, lateral); anterodorsal prefrontal process distinct from, but not extending over, anteroventral process.



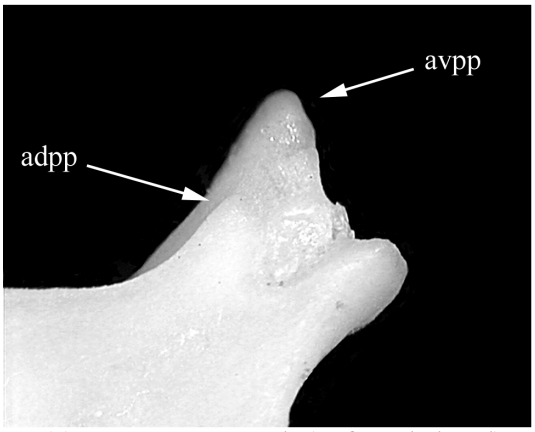
139(2): CJB 1062, *pricei* (rt. frontal, dorsal); anterodorsal prefrontal process fused with anteroventral process.



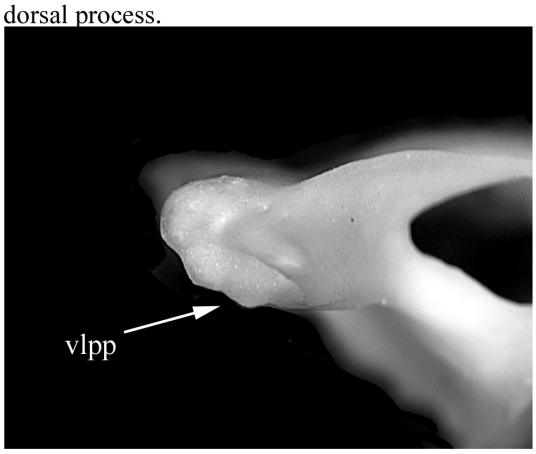
139(2): CJB 1062, *pricei* (rt. frontal, lateral); anterodorsal prefrontal process fused with anteroventral process.



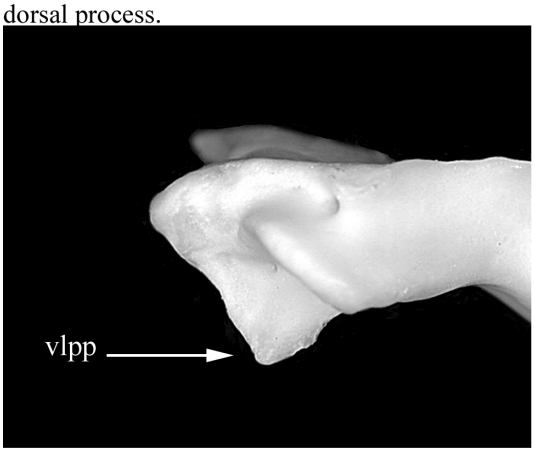
140(0): CJB 001, *atrox* (rt. frontal, dorsal); anteriormost point of anteroventral prefrontal process medial or equal with anteriormost point of anterodorsal process.



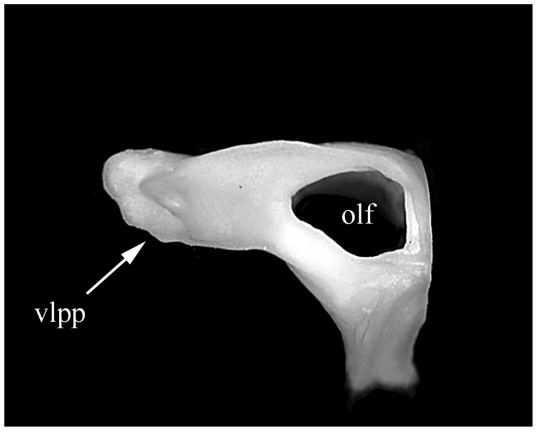
140(1): CJB 694, *contortrix* (rt. frontal, dorsal); anteriormost point of anteroventral prefrontal process lateral to anteriormost point of anterodorsal process.



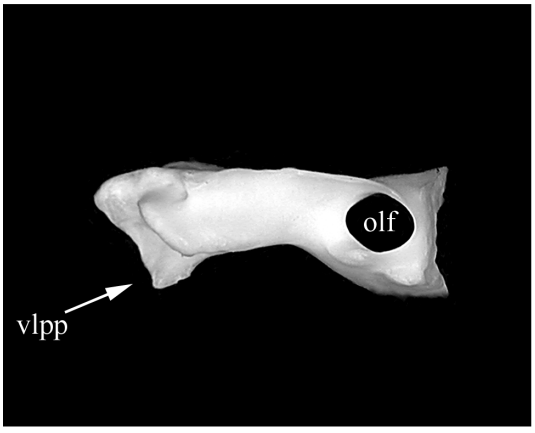
141(0): CJB 715, *contortrix* (rt. frontal, anterior); no pointed or distinct ventrolateral prefrontal process, not triangular shaped.



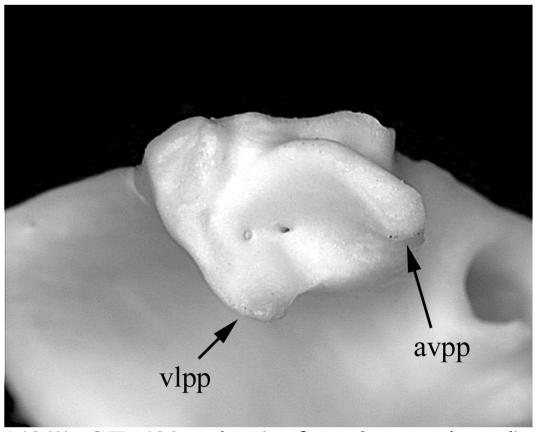
141(1): CJB 490, *ruber* (rt. frontal, anterior); triangular-shaped ventrolateral prefrontal process.



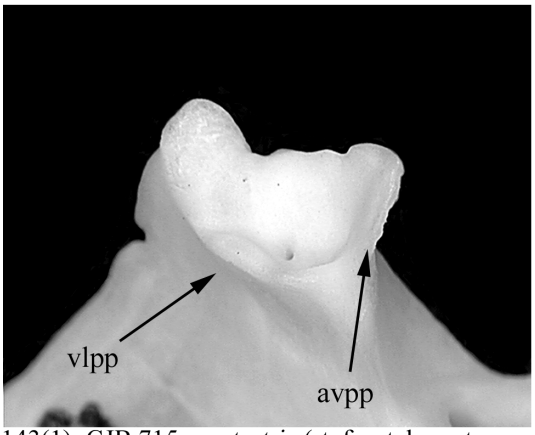
142(0): CJB 715, *contortrix* (rt. frontal, anterior); ventrolateral prefrontal process not ventral to floor of olfactory foramen.



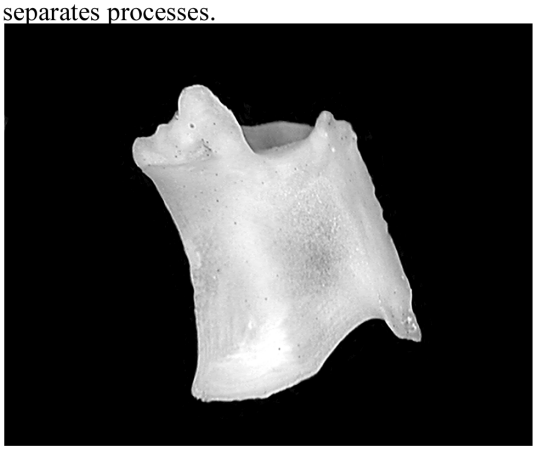
142(1): CJB 490, *ruber* (rt. frontal, anterior); ventrolateral prefrontal process not ventral to floor of olfactory foramen.



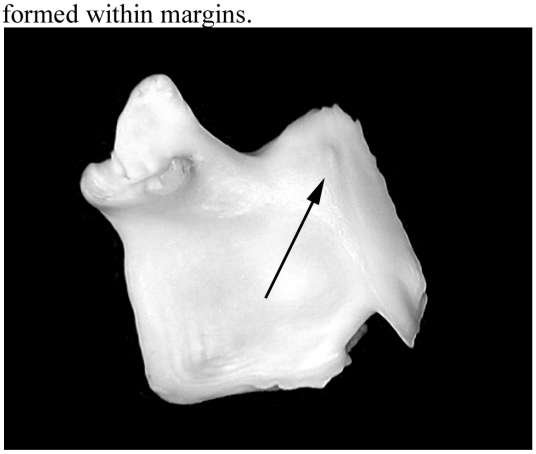
143(0): CJB 490, *ruber* (rt. frontal, ventrolateral); ventrolateral prefrontal process does not connect directly to anteroventral process, large concavity separates processes.



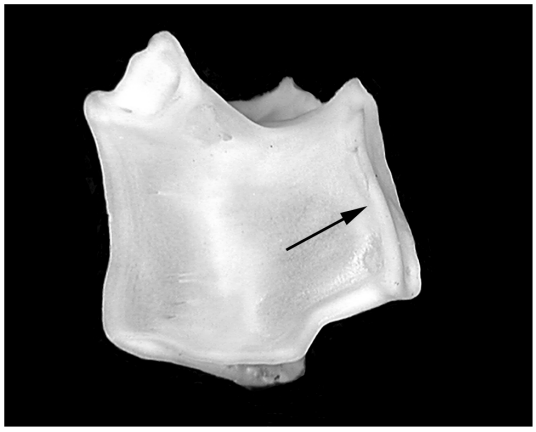
143(1): CJB 715, *contortrix* (rt. frontal, ventrolateral); ventrolateral prefrontal process connects directly to anteroventral process, single cotyle formed within margins.



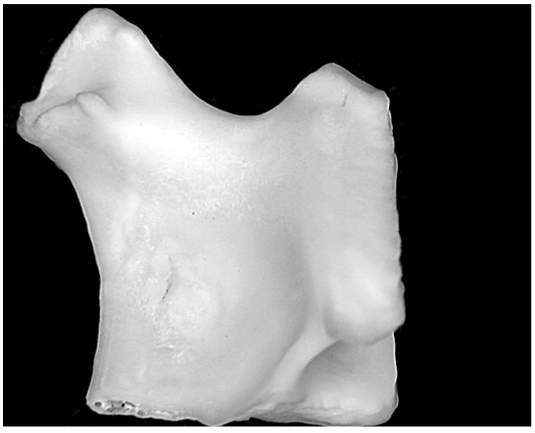
144(0): CJB 1061, *lepidus* (rt. frontal, ventral); vertical ridge or lip absent on ventral surface.



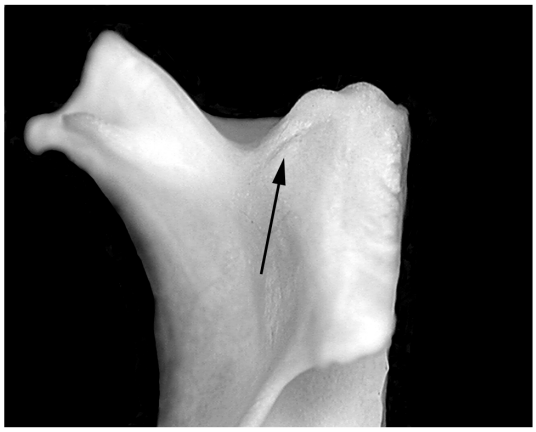
144(1): LSUMZ 29583, *atrox* (rt. frontal, ventral); vertical ridge or lip present, but not entire length of ventral surface.



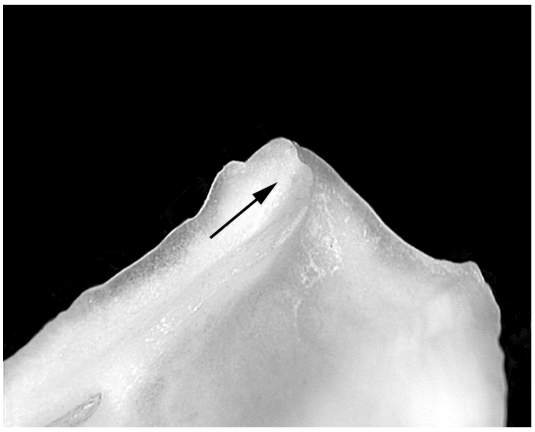
144(2): NAUQSP 14076, *contortrix* (rt. frontal, ventral); vertical ridge or lip present for entire length of ventral surface.



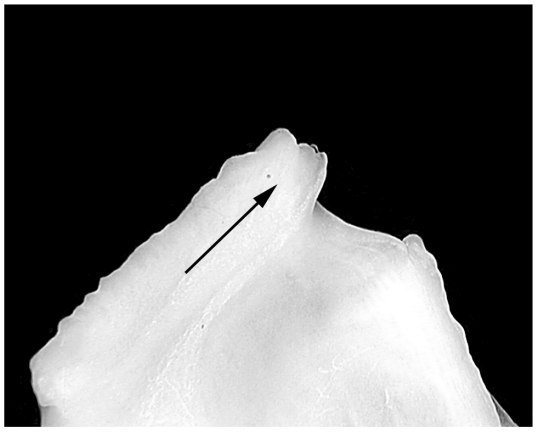
145(0): CJB 577, *atrox* (rt. frontal, ventral); oblique groove in ventral surface, posterior to olfactory foramen, absent.



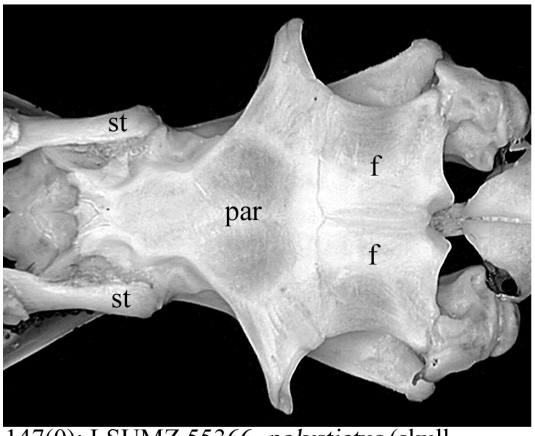
145(1): CJB 650, *cerastes* (rt. frontal, ventral); oblique groove in ventral surface, posterior to olfactory foramen, present.



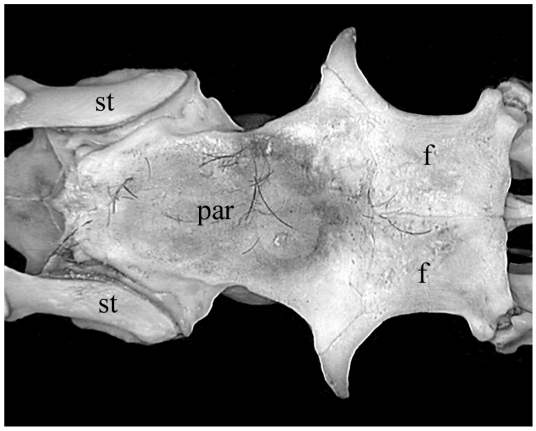
146(0): CJB 715, *contortrix* (rt. frontal, ventral); caudoventral process for basisphenoid articulation present but reduced.



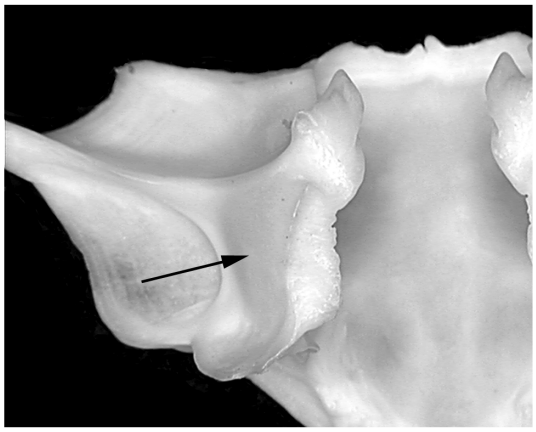
146(1): CJB 490, *ruber* (rt. frontal, ventral); caudoventral process for basisphenoid articulation present as wide process.



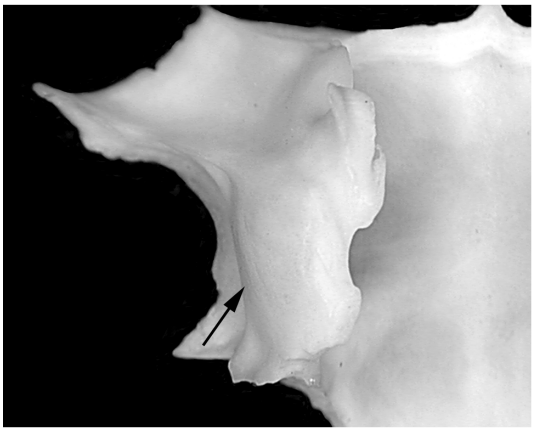
147(0): LSUMZ 55366, *polystictus* (skull, dorsal); minimum width across frontals less than or equal to width of skull at anterior end of supratemporals.



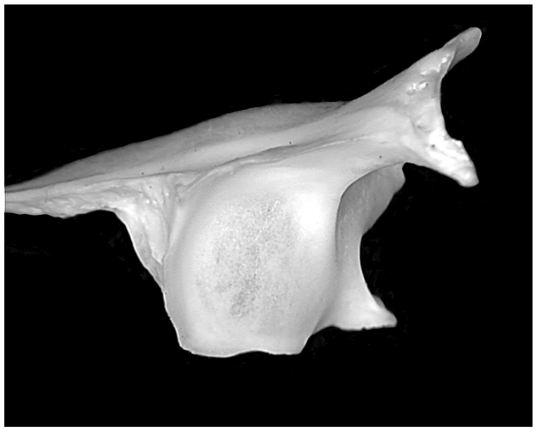
147(1): TCWC 82067, *vegrandis* (skull, dorsal); minimum width across frontals greater than width of skull at anterior end of supratemporals.



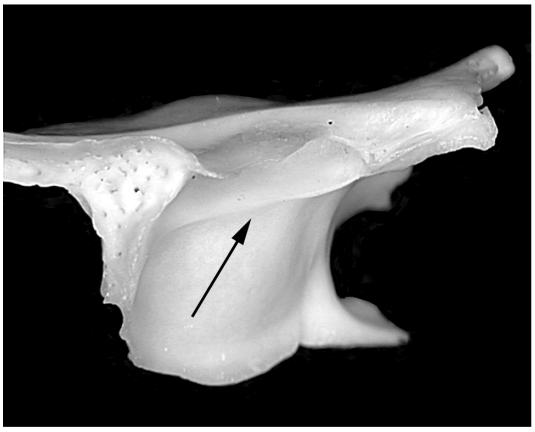
151(0): CJB 001, *atrox* (parietal, ventral); ventrolateral wall moderately convex.



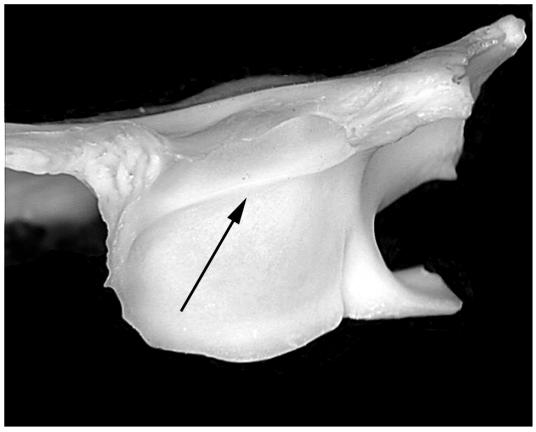
151(1): LSUMZ 10340, *horridus* (parietal, ventral); ventrolateral wall greatly convex.



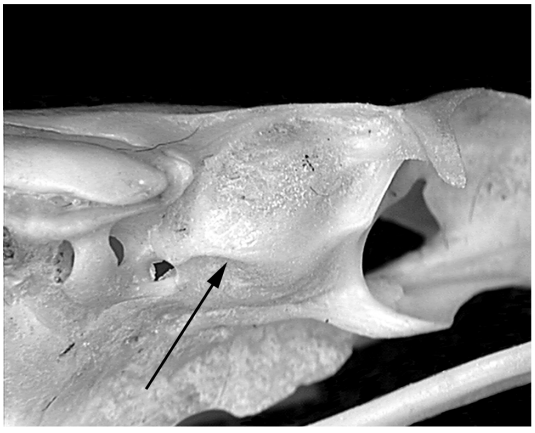
152(0): CJB 577, *atrox* (parietal, lateral); absence of 'secondary' horizontal ridge on lateral parietal wall.



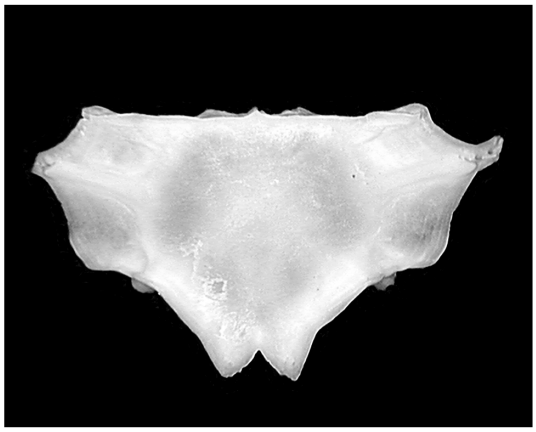
152(1): LSUMZ 29347, *durissus* (parietal, lateral); presence of 'secondary' horizontal ridge on lateral parietal wall.



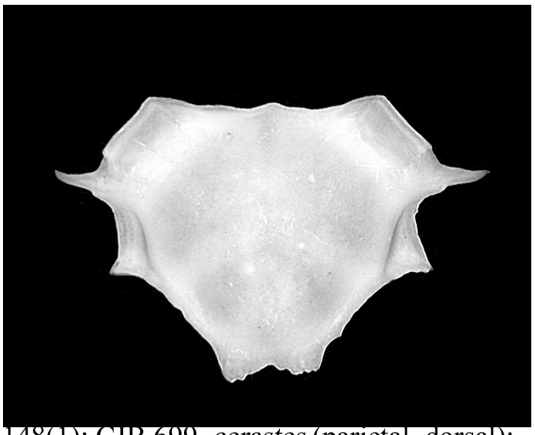
153(0): LSUMZ 29347, *durissus* (parietal, lateral); 'secondary' horizontal ridge present across dorsolateral face of parietal.



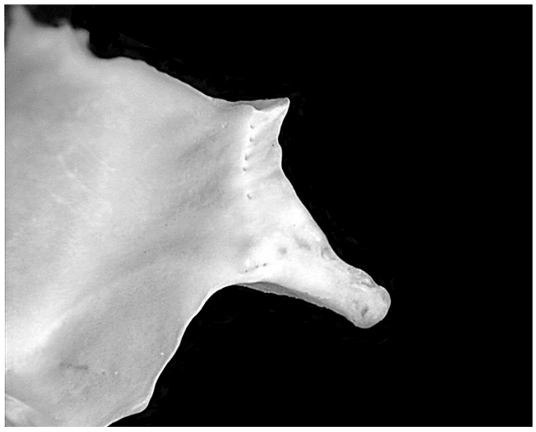
153(1): TCWC 82069, *polystictus* (parietal, lateral); 'secondary' horizontal ridge present across lateroventral face of parietal.



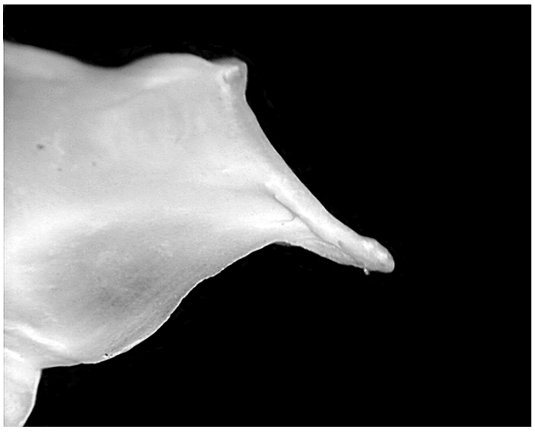
148(0): CJB 001, *atrox* (parietal, dorsal); parietal as wide as long, measured at widest points.



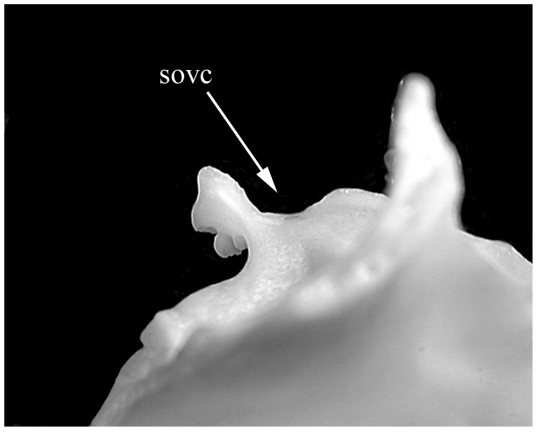
148(1): CJB 699, *cerastes* (parietal, dorsal); parietal longer than wide, measured at widest points.



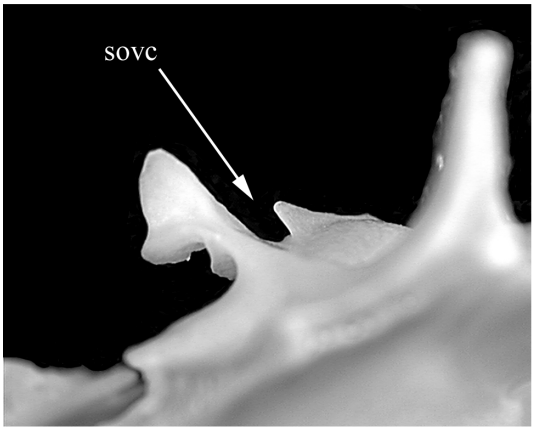
149(0): CJB 577, *atrox* (parietal, lateral); postorbital process without distinct channel or groove for postfrontal.



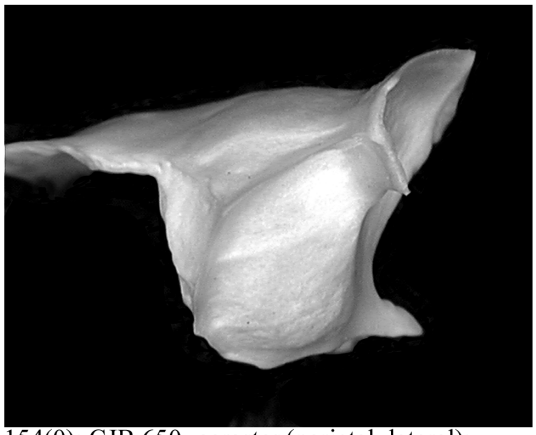
149(1): CJB 001, *atrox* (parietal, lateral); postorbital process with distinct channel or groove for postfrontal.



150(0): CJB 577, *atrox* (parietal, ventrolateral); channel of secondary ant. opening of vidian canal absent or weakly developed.

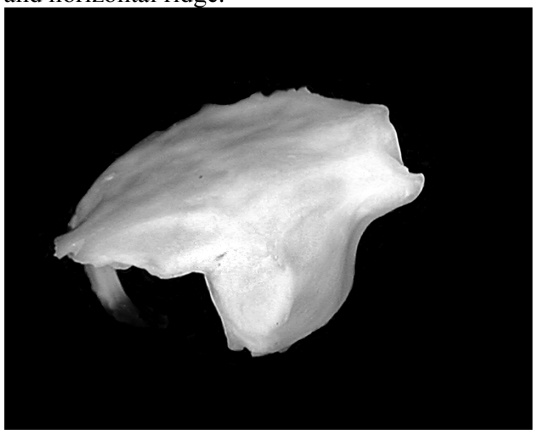


150(0): CJB 490, *atrox* (parietal, ventrolateral); channel of secondary ant. opening of vidian canal strongly developed.

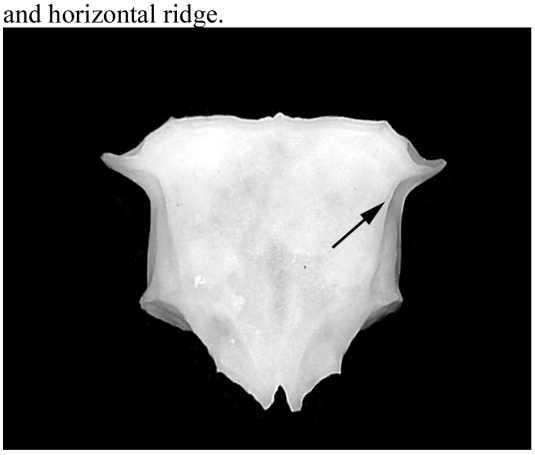


154(0): CJB 650, *cerastes* (parietal, lateral); thickness of dorsolateral horizontal ridge weak, no large recess formed between lateral process and horizontal ridge.

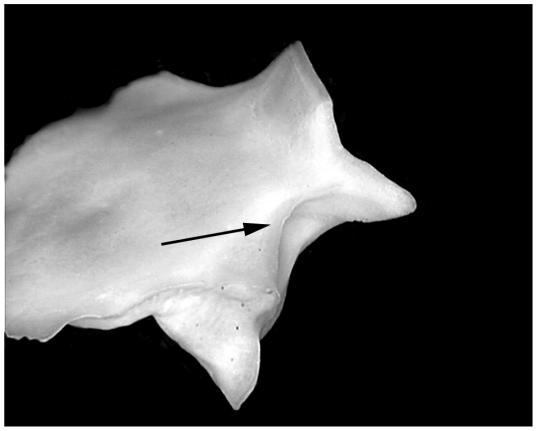
154(1): LSUMZ 29347, *durissus* (parietal, lateral); thickness of dorsolateral horizontal ridge large, creates concavity between lateral process and horizontal ridge.



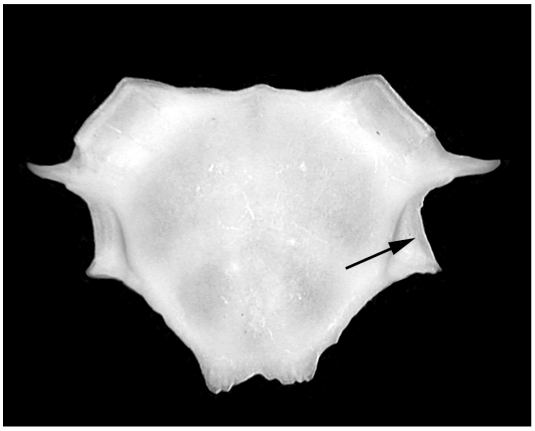
155(0): CJB 1062, *pricei* (parietal, postero-lateral); lateral process absent or only small ridge of bone - does not form a shelf.



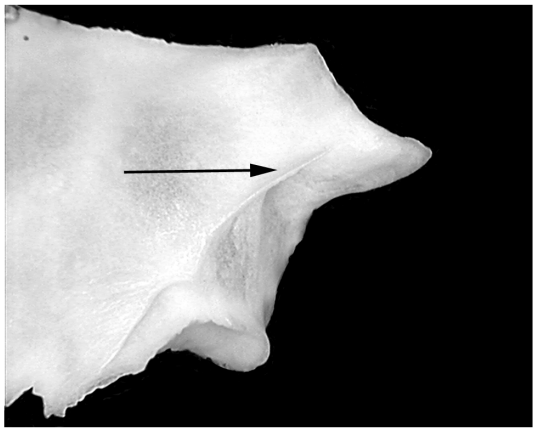
155(0): CJB 1062, *pricei* (parietal, dorsal); lateral process absent or only small ridge of bone - does not form a shelf.



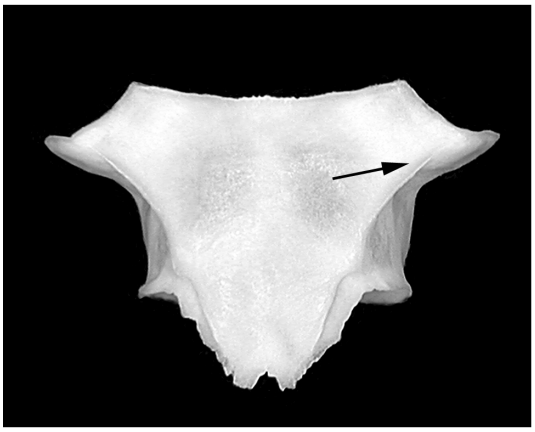
155(1): CJB 699, *cerastes* (parietal, postero-lateral); lateral process small - not attached to postfrontal process.



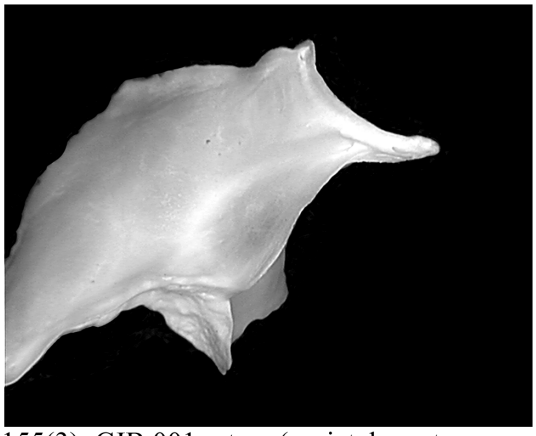
155(1): CJB 699, *cerastes* (parietal, dorsal); lateral process small - not attached to post-frontal process.



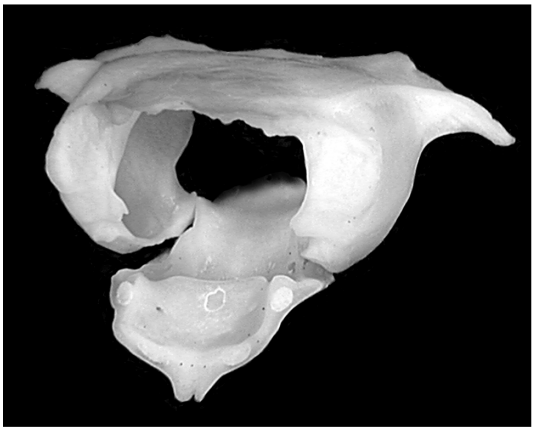
155(2): CJB 694, *contortrix* (parietal, posterolateral); lateral process small, but attached to postfrontal process.



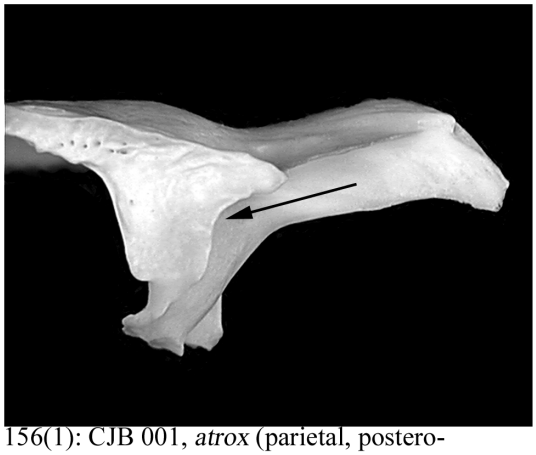
155(2): CJB 694, *contortrix* (parietal, dorsal); lateral process small, but attached to postfrontal process.



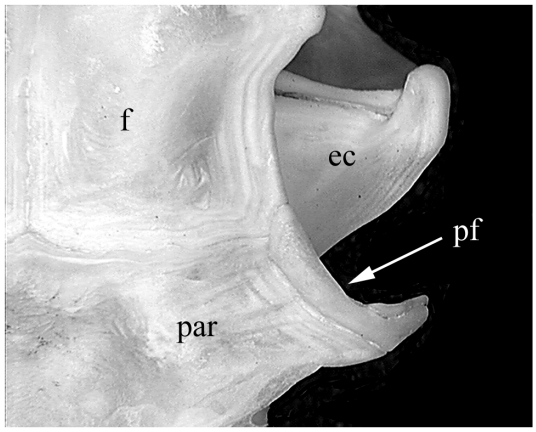
155(3): CJB 001, *atrox* (parietal, postero-lateral); lateral process large, attached to postfrontal process.



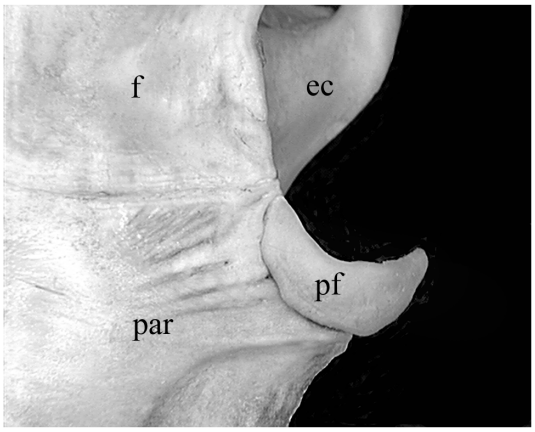
156(0): CJB 1060, *lepidus* (parietal, postero-lateral); vertical/oblique thin lateral shelf absent forming posterior margin with prootic.



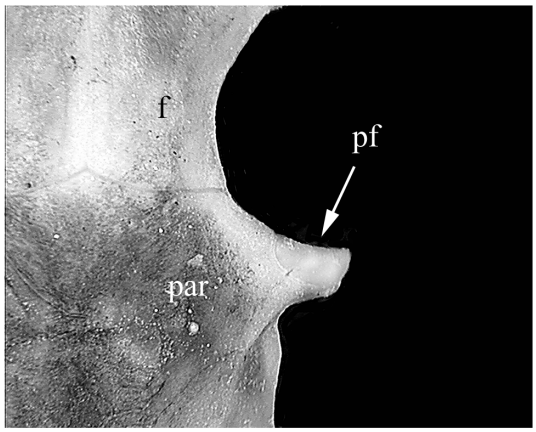
156(1): CJB 001, *atrox* (parietal, postero-lateral); vertical/oblique thin lateral shelf present forming posterior margin with prootic.



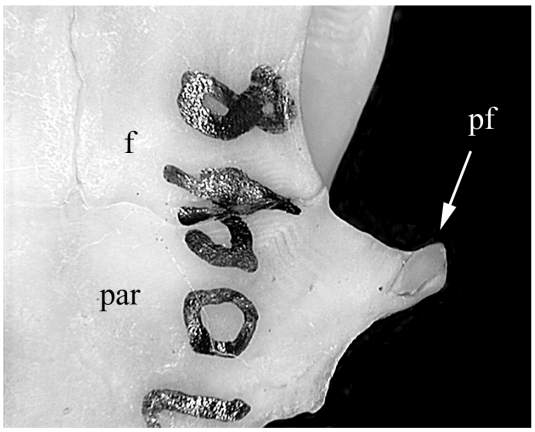
157(0): CJB 070, *durissus* (skull, dorsal); postfrontal contacts frontal, parietal does not form portion of orbit margin.



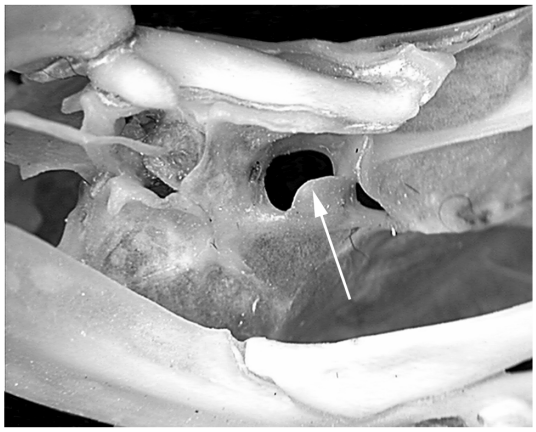
157(1): TJL 930, *polystictus* (skull, dorsal); postfrontal does not contact frontal, parietal forms less than 1/3 posterior orbit margin.



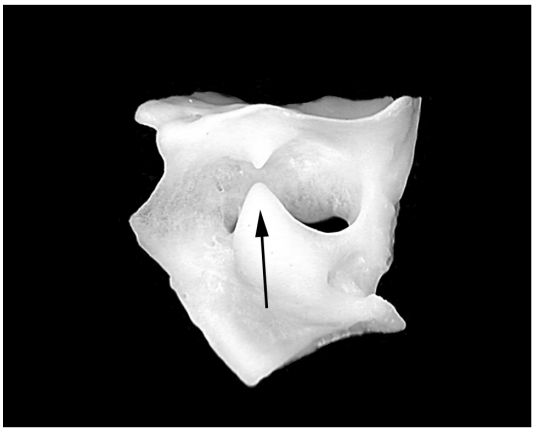
157(2): LSUMZ 42125, *triseriatus* (skull, dorsal); postfrontal does not contact frontal, parietal forms between 1/3 and 2/3 posterior orbit margin.



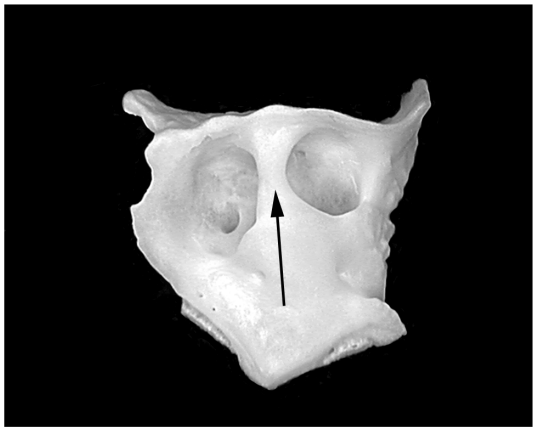
157(3): FMNH 37048, *pusillus* (skull, dorsal); postfrontal does not contact frontal, parietal forms between 1/3 and 2/3 posterior orbit margin.



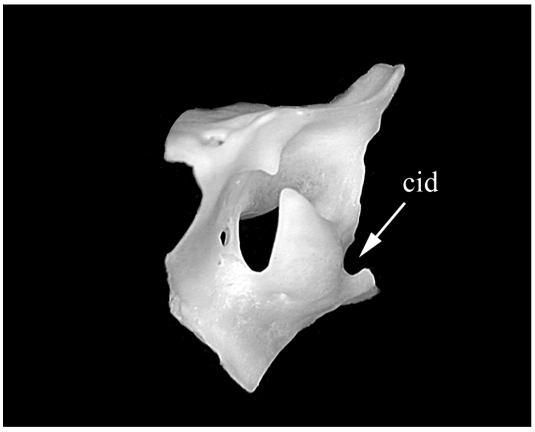
158(0): SDNHM 66333, *unicolor* (skull, lateral); trigeminal foramen not separated by a bony partition.



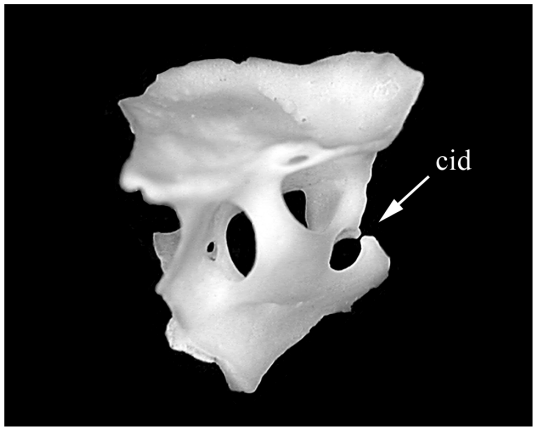
158(1): CJB 577, *atrox* (rt. prootic, lateral); trigeminal foramen separated by incomplete bony partition.



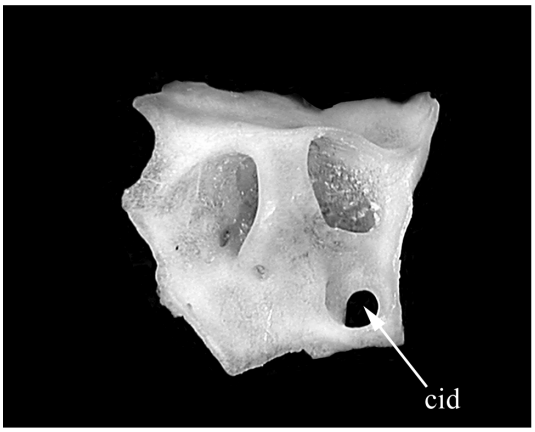
158(2): CJB 001, *atrox* (rt. prootic, lateral); trigeminal foramen separated by complete bony partition.



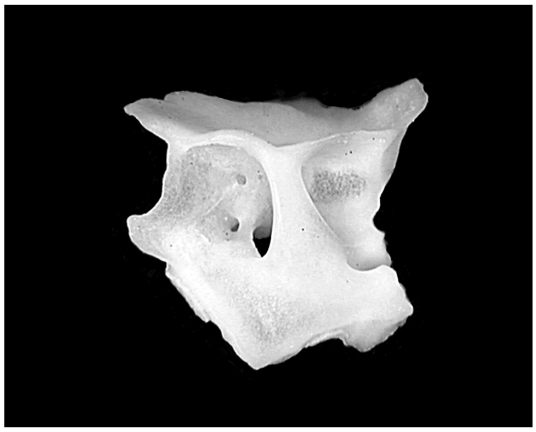
159(0): CJB 577, *atrox* (rt. prootic, lateral); foramen for re-entry of CID nerve, margin shared ~50% with parietal.



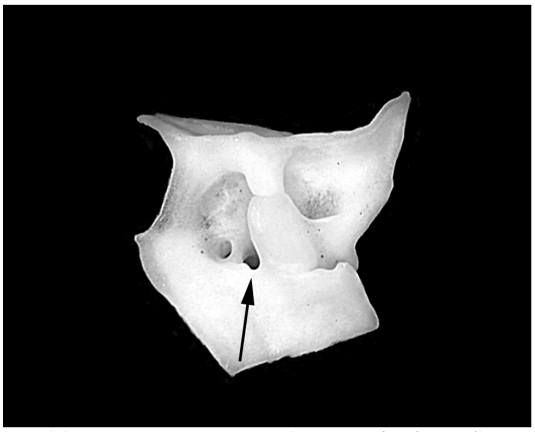
159(1): LSUMZ 10340, *horridus* (rt. prootic, lateral); foramen for re-entry of CID nerve, greater than 90% of margin within prootic.



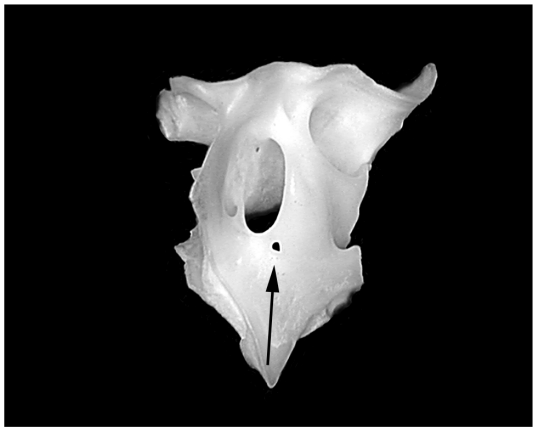
159(2): NAUQSP 7381, *tigris* (rt. prootic, lateral); foramen for re-entry of CID nerve, margin entirely enclosed within prootic.



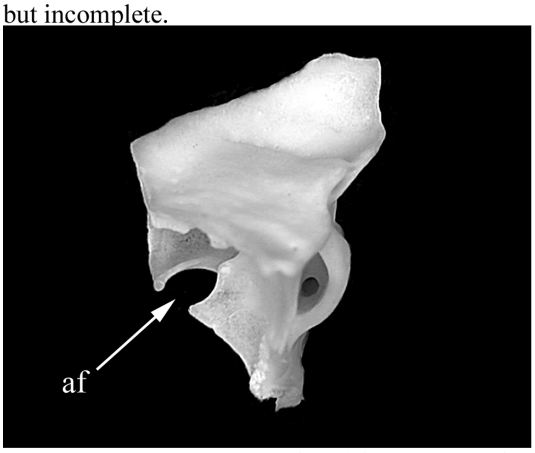
160(0): CJB 1061, *lepidus* (rt. prootic, lateral); separate foramen for posterior branch of pterygoid division of trigeminal absent.



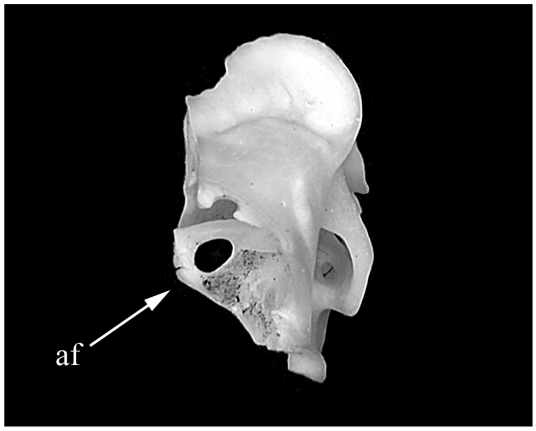
160(1): CJB 699, *cerastes* (rt. prootic, lateral); separate foramen for posterior branch of pterygoid division of trigeminal present, but incomplete.



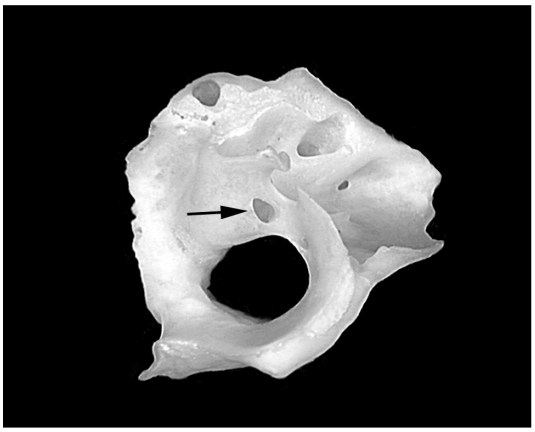
160(2): CJB 001, *atrox* (rt. prootic, lateral); separate foramen for posterior branch of pterygoid division of trigeminal present.



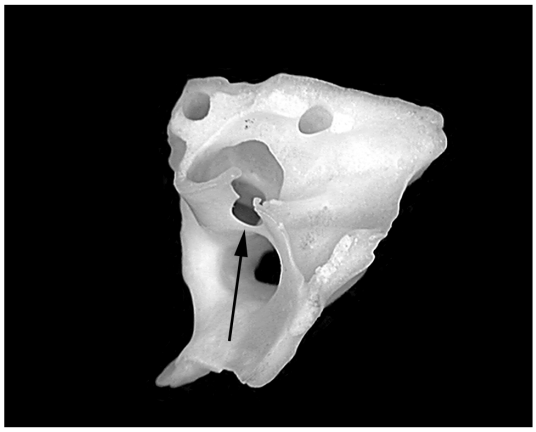
161(0): LSUMZ 10340, *horridus* (rt. prootic, posterolateral); auditory foramen not complete, otooccipital forms posterior margin.



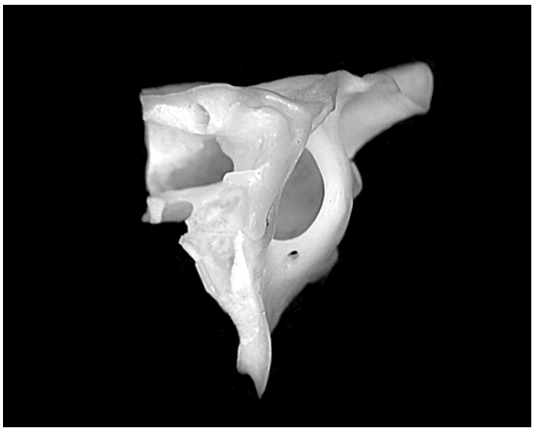
161(1): TJL 930, *polystictus* (rt. prootic, posterolateral); auditory foramen completely enclosed within prootic.



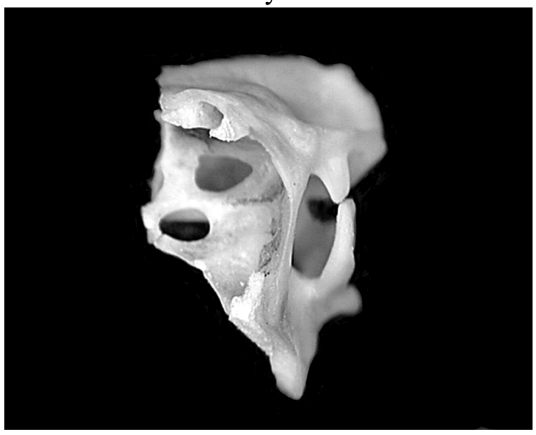
162(0): CJB 001, *atrox* (rt. prootic, posteromedial); interior foramen (anterior of auditory foramen) complete and entire.



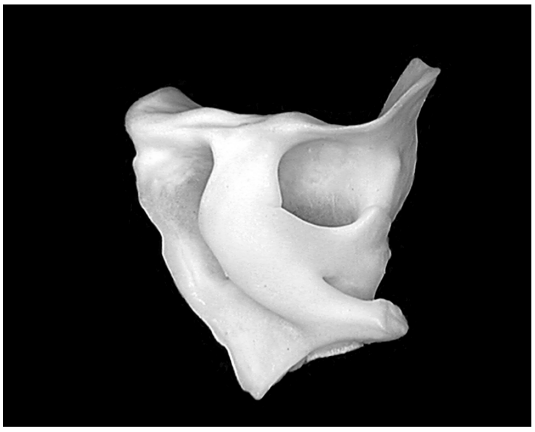
162(1): LSUMZ 10340, *horridus* (rt. prootic, posteromedial); interior foramen incomplete, confluent with auditory foramen.



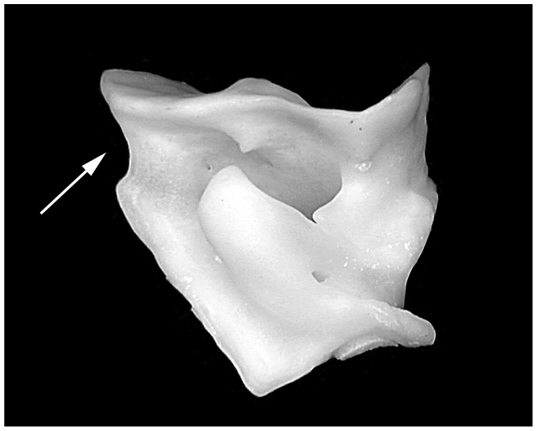
163(0): CJB 001, *atrox* (rt. prootic, posterolateral); anteroposterolateral corner with sharp 90 degree drop to lateral face.



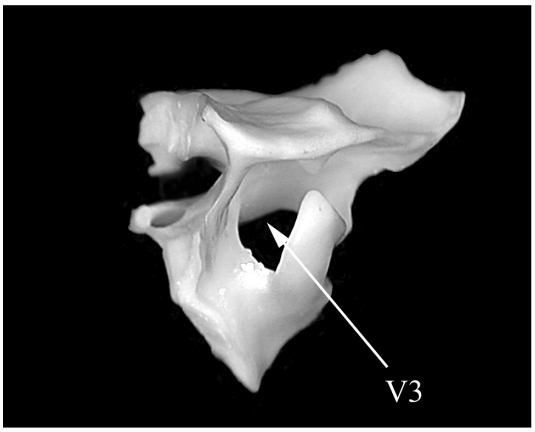
163(1): CJB 1062, *pricei* (rt. prootic, posterolateral); anteroposterolateral corner with no sharp 90 degree drop to lateral face.



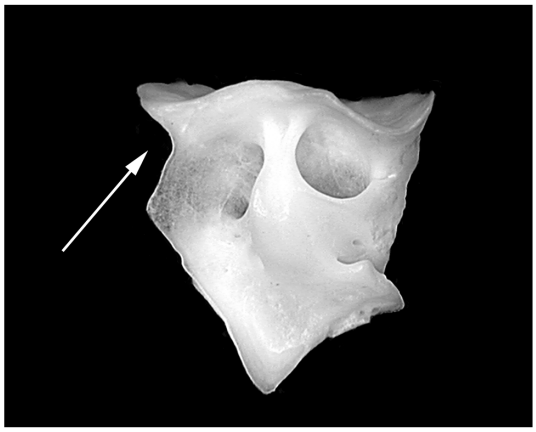
164(0): LSUMZ 29584, *adamanteus* (rt. prootic, lateral); anteroposterolateral edge not concave.



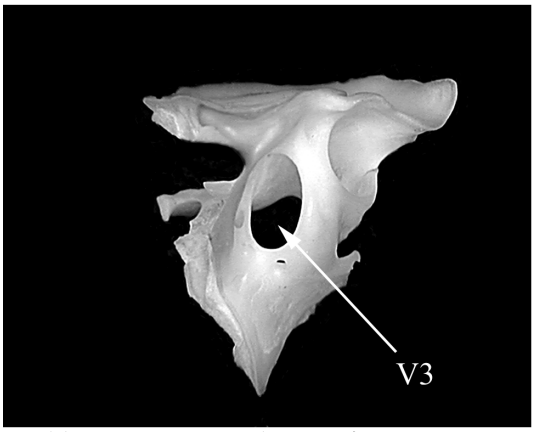
164(1): LSUMZ 29583, *atrox* (rt. prootic, lateral); anteroposterolateral edge moderately concave, depth less than 1/2 width of V3 foramen.



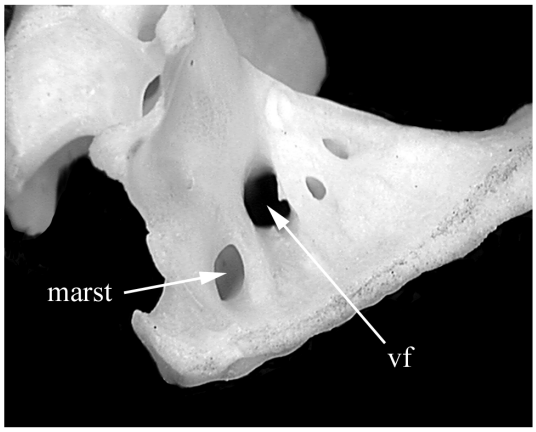
164(1): LSUMZ 29583, *atrox* (rt. prootic, posterolateral); anteroposterolateral edge moderately concave, depth less than 1/2 width of V3 foramen.



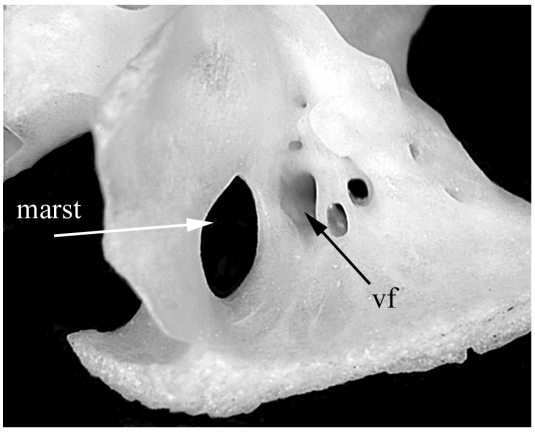
164(2): CJB 001, *atrox* (rt. prootic, lateral); anteroposterolateral edge strongly concave, depth greater than 1/2 width of V3 foramen.



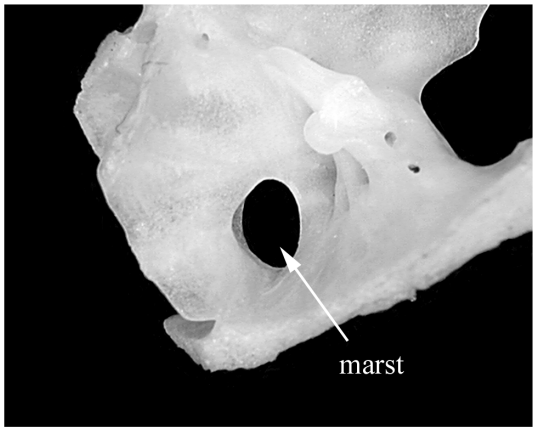
164(2): CJB 001, *atrox* (rt. prootic, postero-lateral); anteroposterolateral edge strongly concave, depth greater than 1/2 width of V3 foramen.



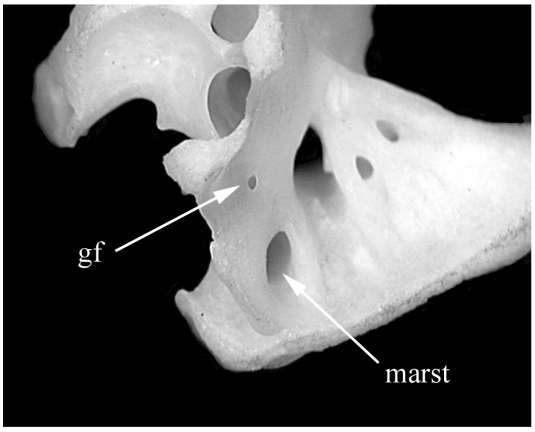
165(0): CJB 001, *atrox* (rt. otooccipital, anteromedial); size of MARST less than or equal to medial aperature of vagus nerve.



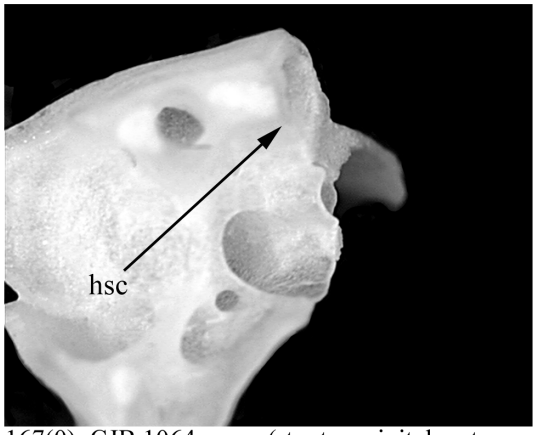
165(1): LSUMZ 29347, *durissus* (rt. otooccipital, anteromedial); size of MARST greater than medial aperature of vagus nerve.



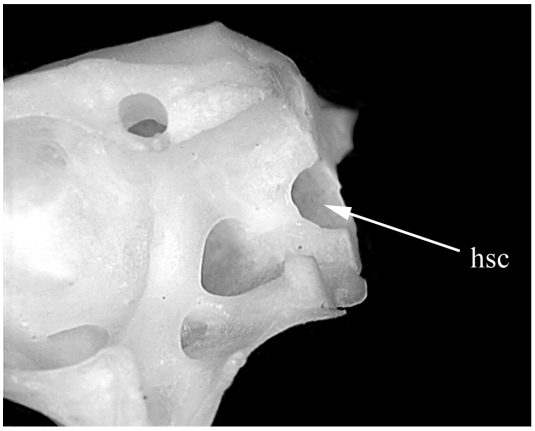
166(0): LSUMZ 29347, *durissus* (rt. otooccipital, anteromedial); separate foramen for glossopharyngeal nerve absent.



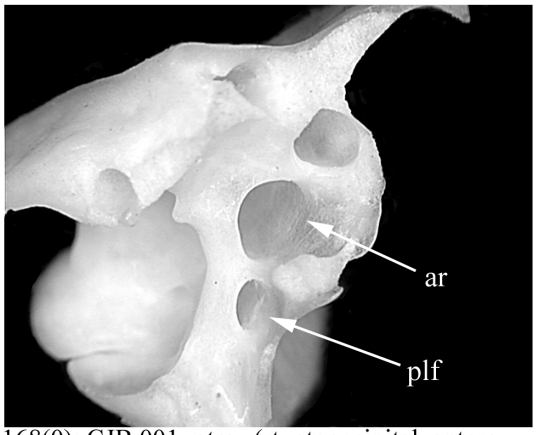
166(1): CJB 001, *atrox* (rt. otooccipital, anteromedial); separate foramen for glossopharyngeal nerve present.



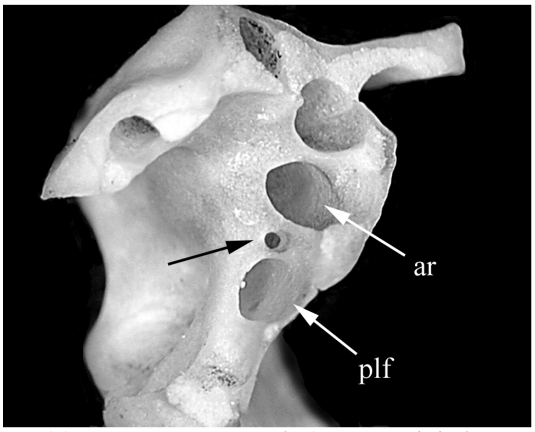
167(0): CJB 1064, *enyo* (rt. otooccipital, anteromedial); margin of horizontal semicircular canal mostly entire or continuous to supraoccipital articulation.



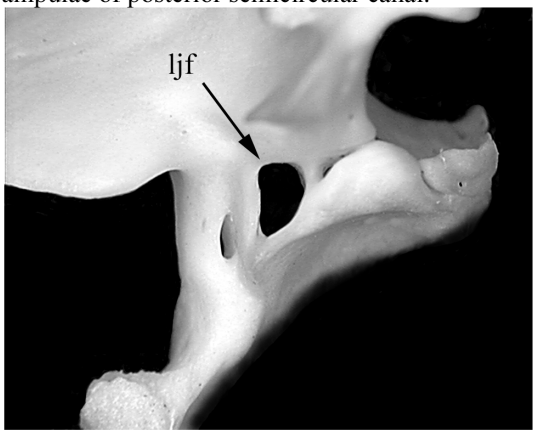
167(1): CJB 001, *atrox* (rt. otooccipital, anteromedial); margin of horizontal semicircular canal not continuous to supraoccipital articulation, portion of margin absent.



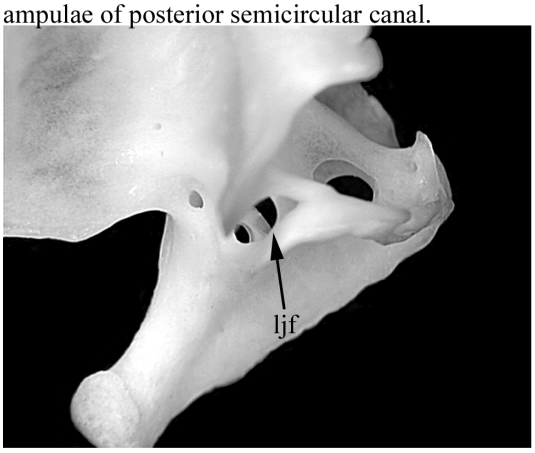
168(0): CJB 001, *atrox* (rt. otooccipital, antero-lateral); absence of small foramen between peri-lymphatic and posterior ampullary recess for ampulae of posterior semicircular canal.



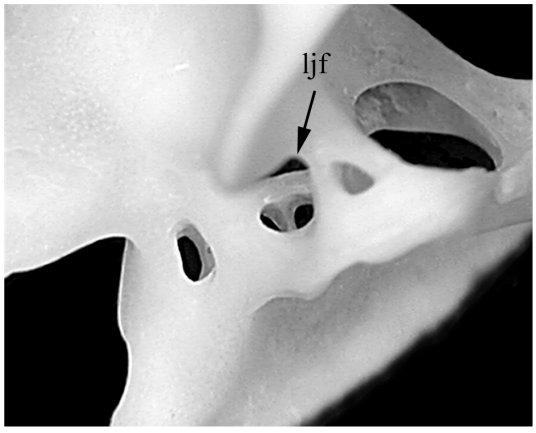
168(1): CJB 715, *contortrix* (rt. otooccipital, anterolateral); presence of small foramen between perilymphatic and posterior ampullary recess for ampulae of posterior semicircular canal.



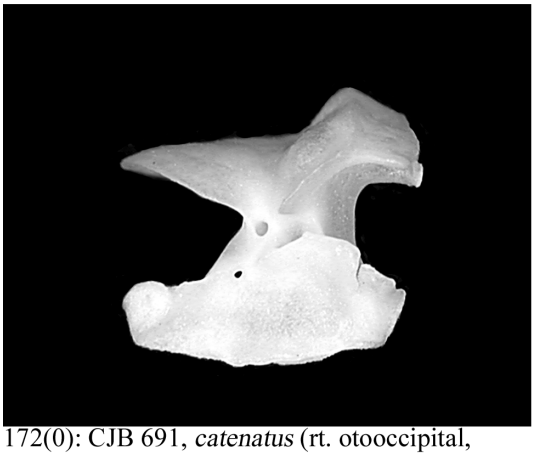
171(0): CJB 490, *ruber* (rt. otooccipital, antero-medial); lateral jugular foramen with no other foramen present.



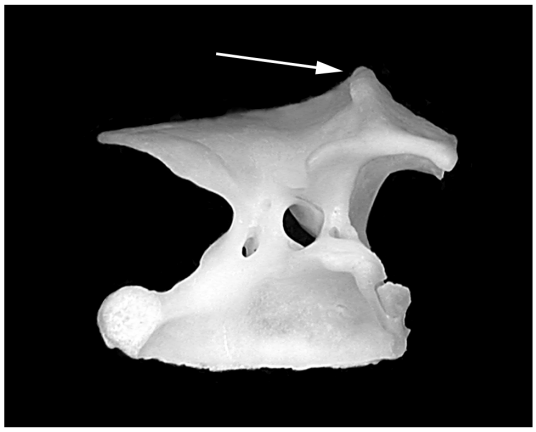
171(1): CJB 001, *atrox* (rt. otooccipital, antero-medial); lateral jugular foramen with one additional foramen present.



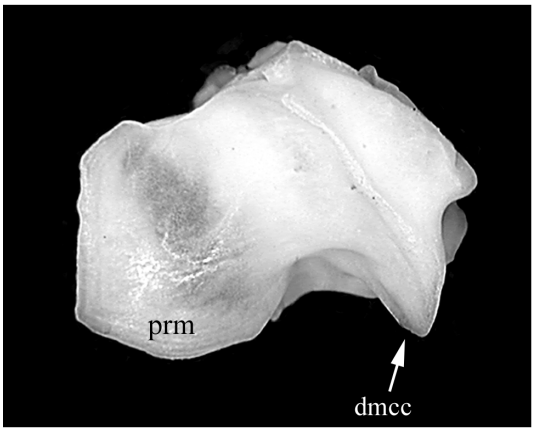
171(2): CJB 577, *atrox* (rt. otooccipital, antero-medial); lateral jugular foramen with two or more additional foramen present.



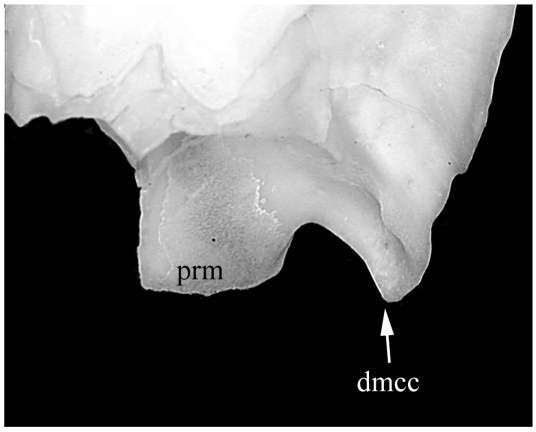
172(0): CJB 691, *catenatus* (rt. otooccipital, posterior); rounded surface (no sharp 90 degree angle) at transition between lower/upper dorsal surface.



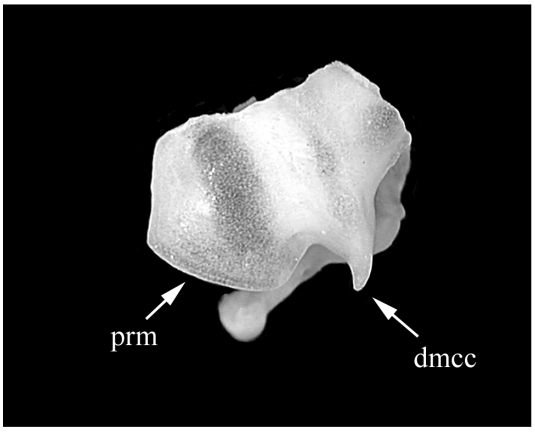
172(1): CJB 577, *atrox* (rt. otooccipital, posterior); sharp transition between lower/upper dorsal surface.



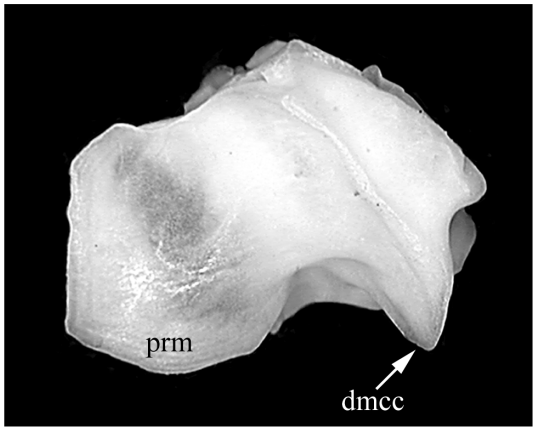
173(0): CJB 001, *atrox* (rt. otooccipital, dorsal); extension of dorsal margin of crista circumfenestralis not past posterior roof margin.



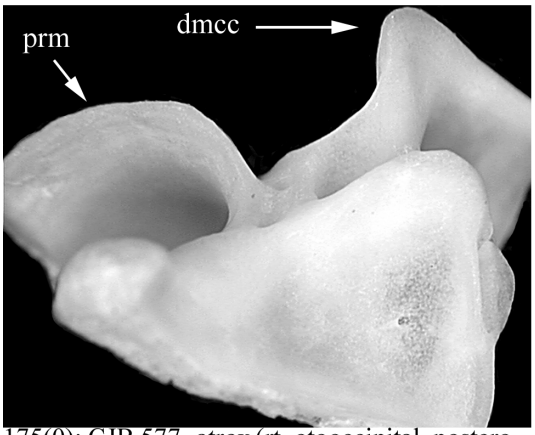
173(1): NAUQSP 14086, *basiliscus* (rt. otooccipital, dorsal); extension of dorsal margin of crista circumfenstralis past posterior roof margin.



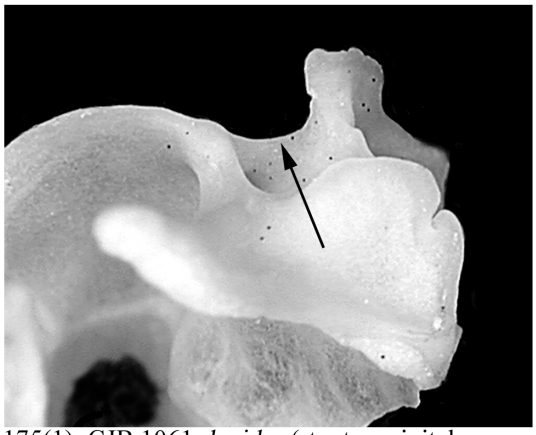
174(0): CJB 1059, *pricei* (rt. otooccipital, dorsal); extension of dorsal margin of crista circumfenestralis narrow and peg-like or crescent-shaped.



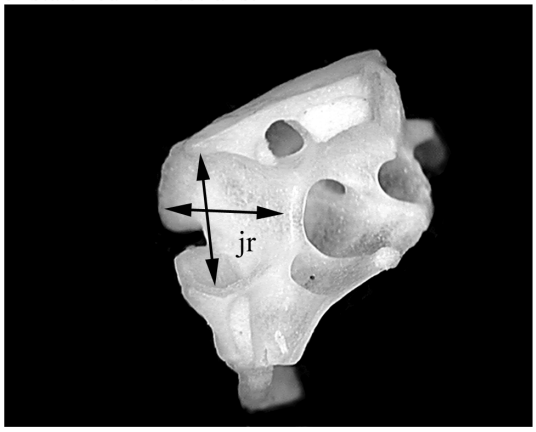
174(1): CJB 001, *atrox* (rt. otooccipital, dorsal); extension of dorsal margin of crista circumfenestralis not narrow and peg-like or crescent-shaped.



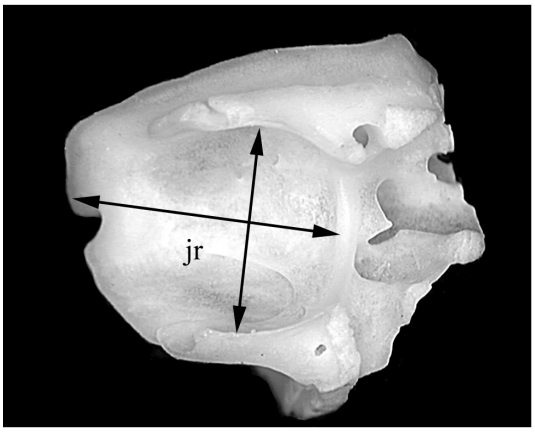
175(0): CJB 577, *atrox* (rt. otooccipital, posteroventral); horizontal shelf absent between posteroir dorsal margin and dorsal margin of crista circumfenestralis.



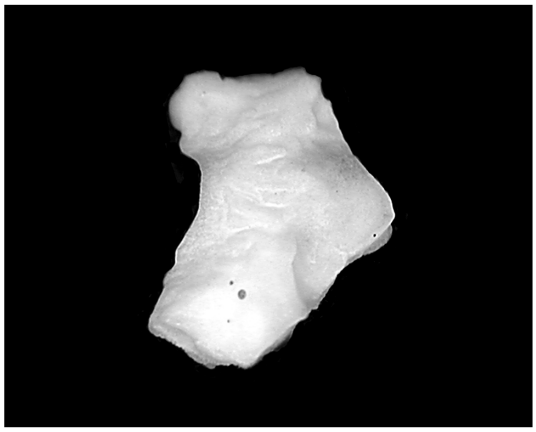
175(1): CJB 1061, *lepidus* (rt. otooccipital, posteroventral); horizontal shelf present between posteroir dorsal margin and dorsal margin of crista circumfenestralis.



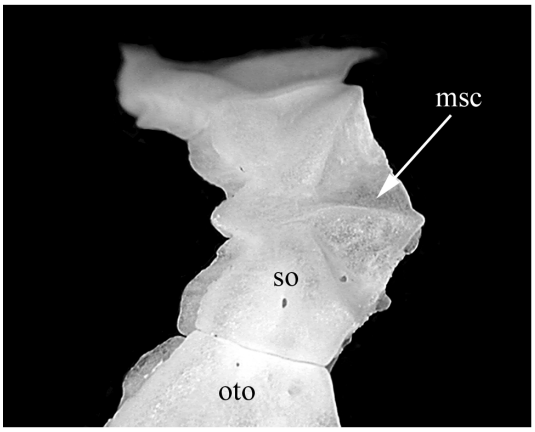
176(1): CJB 001, *atrox* (rt. otooccipital, anteromedial); juxtapedial recess not longer than tall.



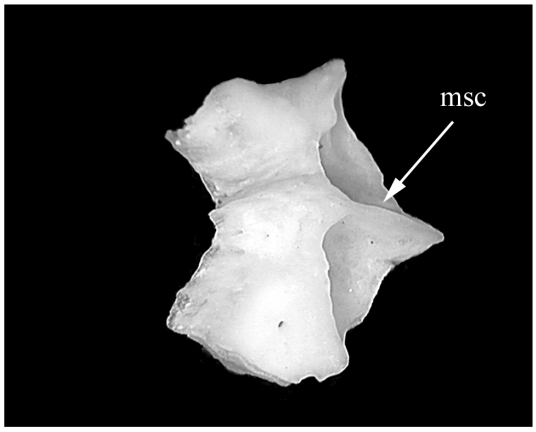
176(0): CJB 490, *ruber* (rt. otooccipital, anteromedial); juxtapedial recess longer than tall.



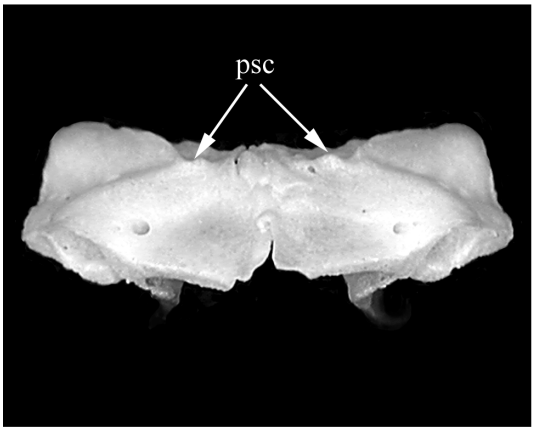
177(0): CJB 699, *cerastes* (supratemporal, dorsolateral); defined midsagittal crest absent.



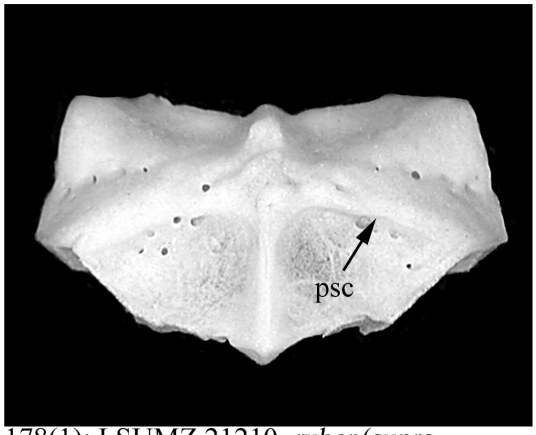
177(1): CJB 1064, *enyo* (supratemporal, dorsolateral); defined midsagittal crest present, but not to tip of posterior process.



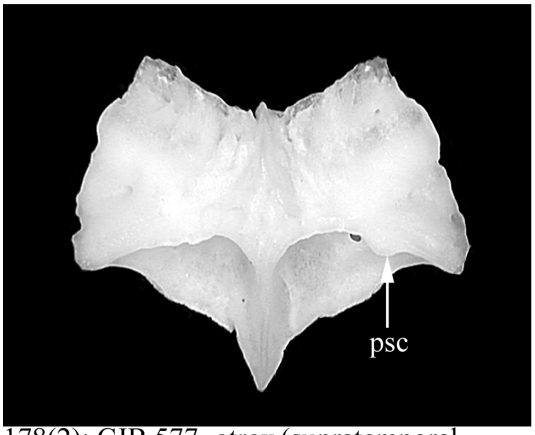
177(2): CJB 577, *atrox* (supratemporal, dorsolateral); defined midsagittal crest present to tip of posterior process.



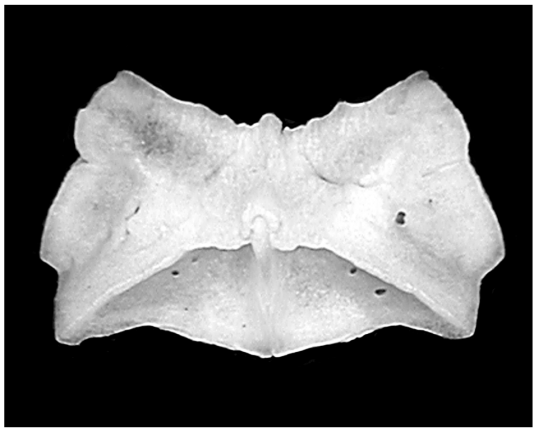
178(0): CJB 690, *cerastes* (supratemporal, posterodorsal); parasagittal crests present only as rounded edges, nothing distinct.



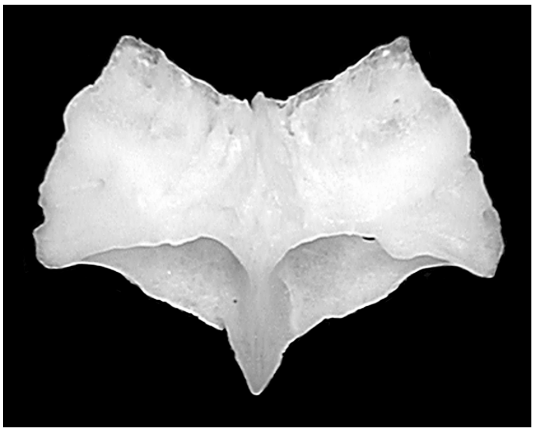
178(1): LSUMZ 21210, *ruber* (supra-temporal, posterodorsal); parasagittal crests distinct, but not entire width of bone.



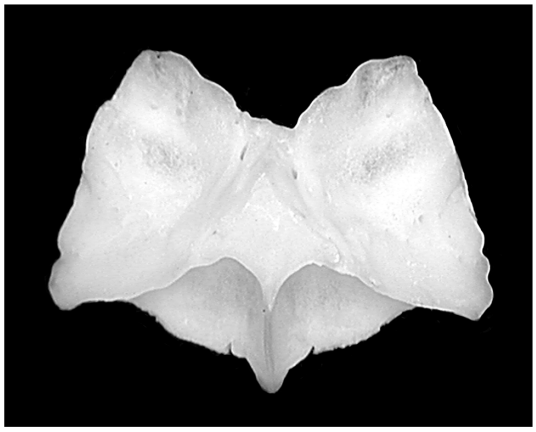
178(2): CJB 577, *atrox* (supratemporal, dorsal); parasagittal crests distinct entire width of bone.



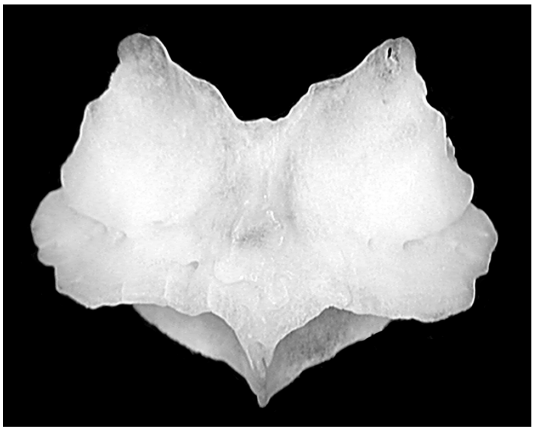
179(0): CJB 715, *contortrix* (supraoccipital, dorsal); posterior margin with no well-defined point, more rounded than pointed.



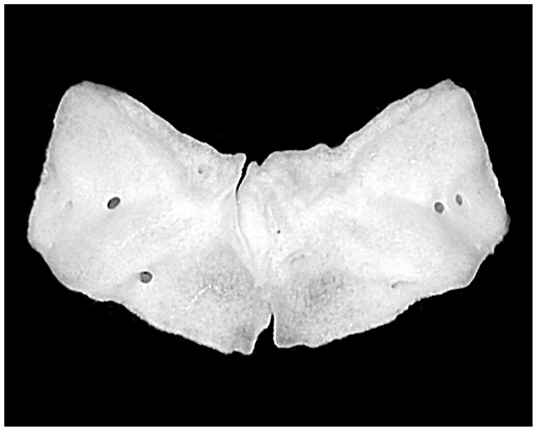
179(1): CJB 577, *atrox* (supraoccipital, dorsal); posterior margin with well-defined, distinct process.



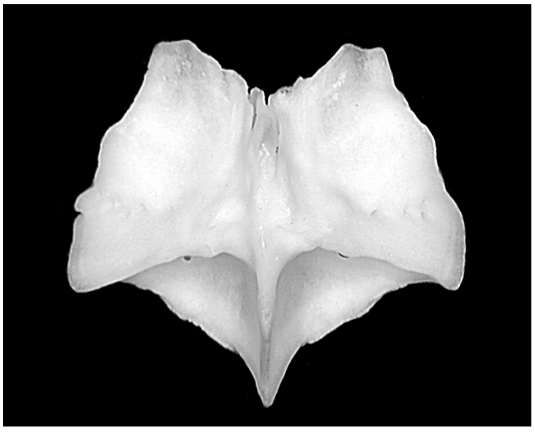
180(0): CJB 001, *atrox* (supratemporal, dorsal); width of dorsal roof along midline less than 1/2 length at widest length.



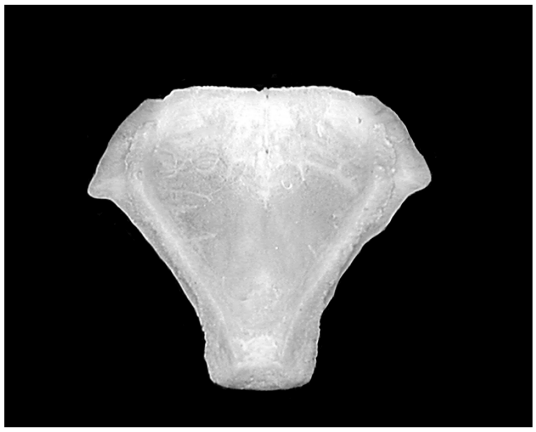
180(1): CJB 490, *ruber* (supratemporal, dorsal); width of dorsal roof along midline greater than 1/2 length at widest length.



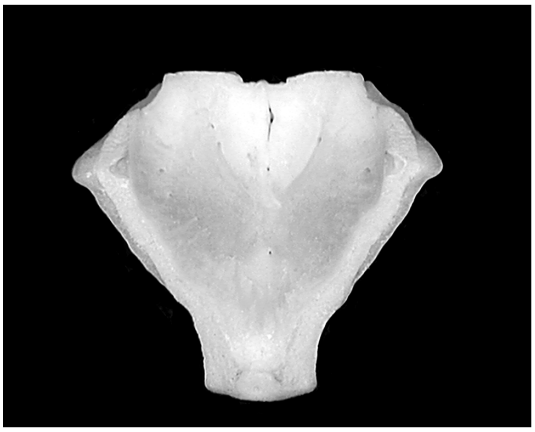
181(0): CJB 650, *cerastes* (supratemporal, dorsal); ratio of roof length/width: 0.4 smallest ratio.



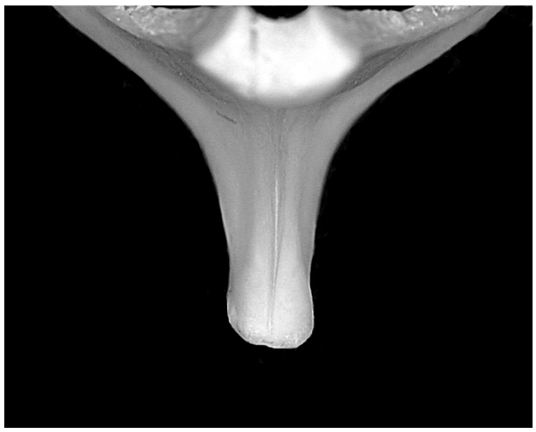
181(0): CM 29583, *atrox* (supratemporal, dorsal); ratio of roof length/width: 0.8 largest ratio.



182(0): CJB 490, *ruber* (basioccipital, dorsal); anterior margin entire.

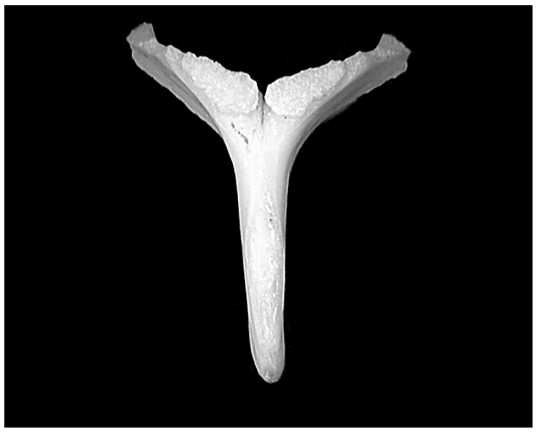


182(1): CJB 001, *atrox* (basioccipital, dorsal); anterior margin notched at midline.

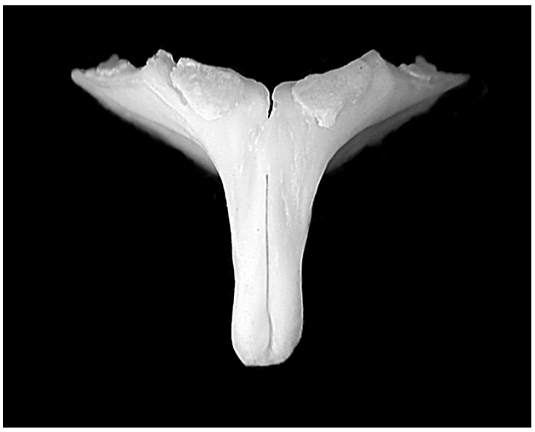


183(0): CJB 577, *atrox* (basioccipital, posterior); distal end of ventral process single, not bifurcated.

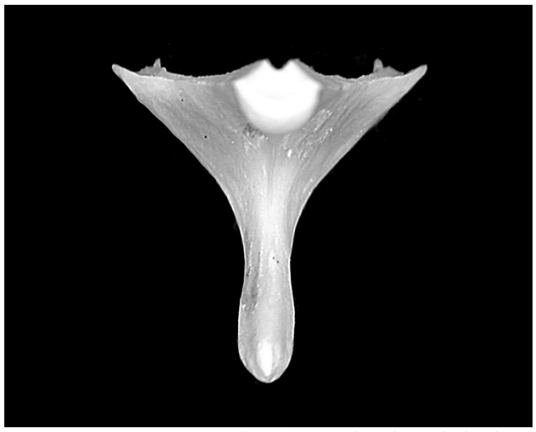
183(1): CJB 490, *ruber* (basioccipital, posterior); distal end of ventral process bifurcated.



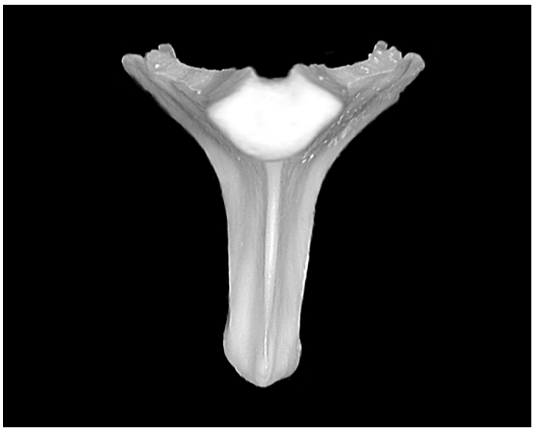
184(0): LSUMZ 29347, *durissus* (basioccipital, anterior); ventral process single solid and fused element.



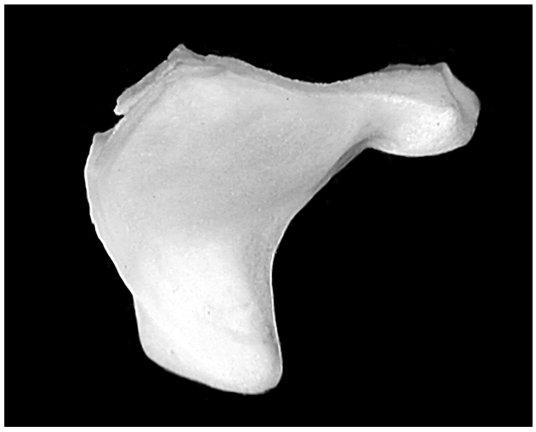
184(1): CJB 001, *atrox* (basioccipital, anterior); two or more distinct elements together comprising ventral process.



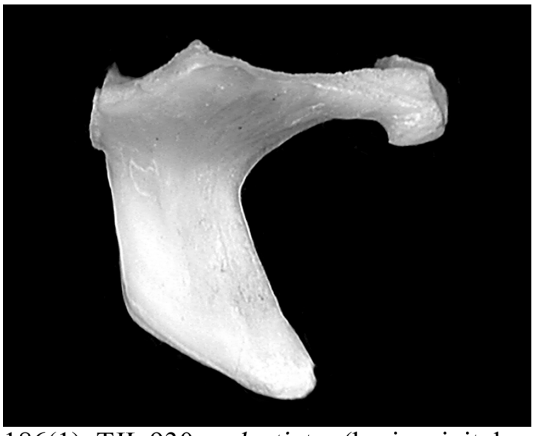
185(0): TJL 930, *polystictus* (basioccipital, posterior); ventral process thin, flat with no anterior lateral struts.



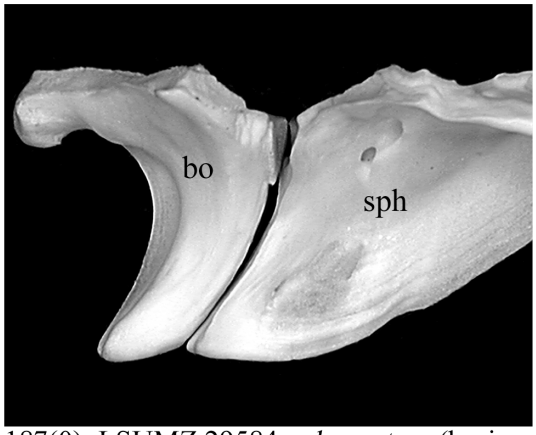
185(1): LSUMZ 29583, *atrox* (basioccipital, posterior); ventral process thick with anterior lateral struts.



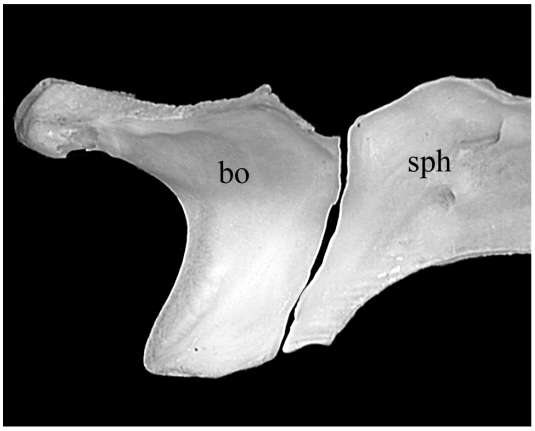
186(0): CJB 508, *piscivorus* (basioccipital, lateral); ventral process does not curve back past its posterodorsal origin.



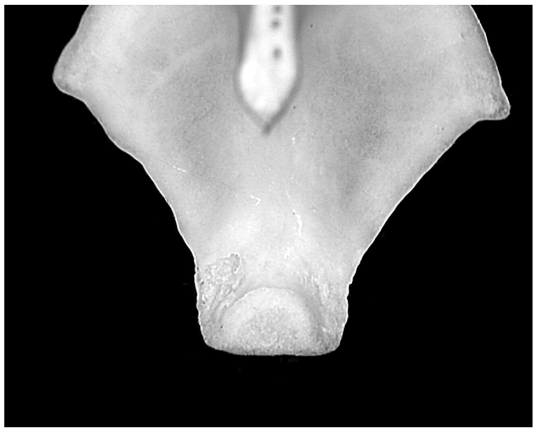
186(1): TJL 930, *polystictus* (basioccipital, lateral); ventral process does curve back past its posterodorsal origin.



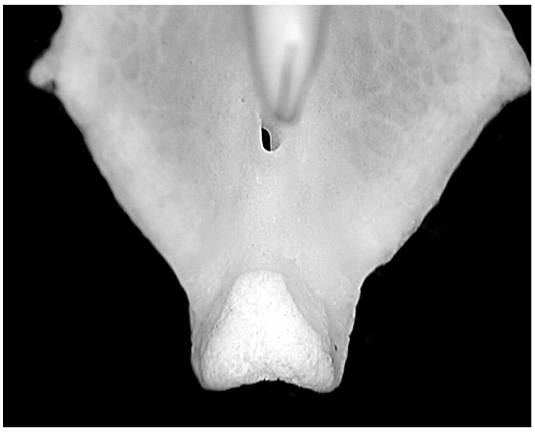
187(0): LSUMZ 29584, *adamanteus* (basioccipital and sphenoid, lateral); basioccipital barely extends further ventrally.



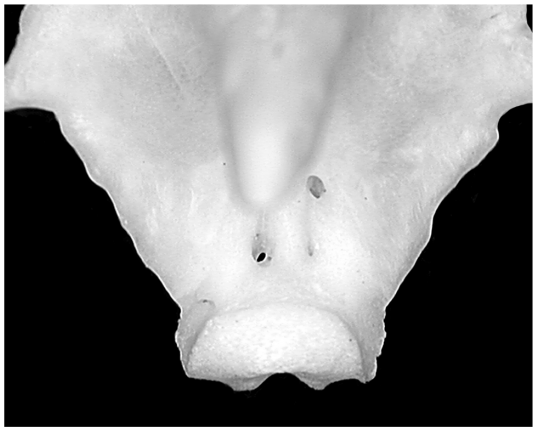
187(1): CJB 001, *atrox* (basioccipital and sphenoid, lateral); basioccipital clearly extends further ventrally, not close.



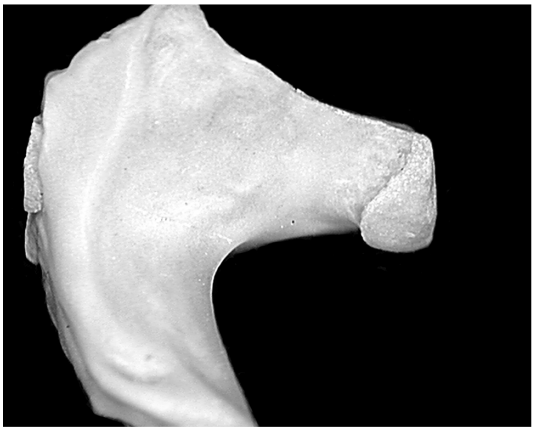
188(0): CJB 574, *atrox* (basioccipital, ventral); no foramen present between ventral and condylar processes.



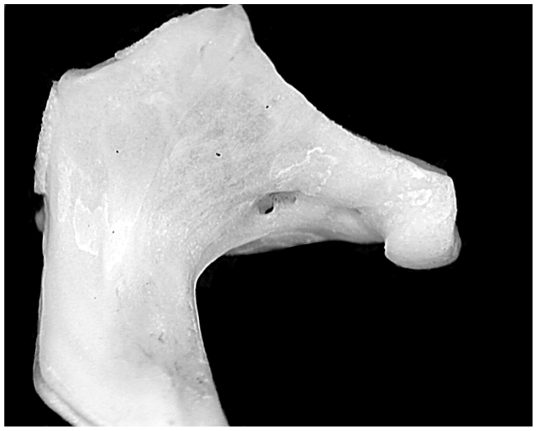
188(1): CJB 490, *ruber* (basioccipital, ventral); single foramen present between ventral and condylar processes.



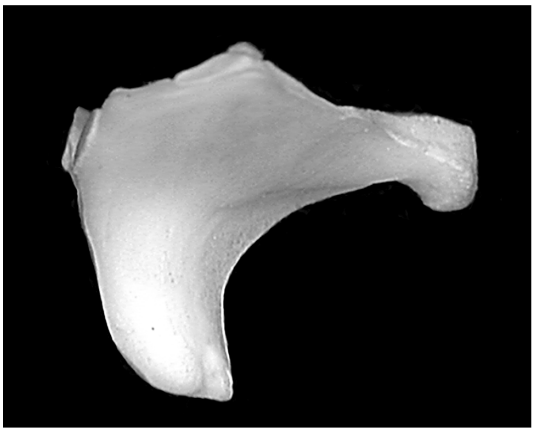
188(2): CJB 692, *bilineatus* (basioccipital, ventral); two or more foramina present between ventral and condylar processes.



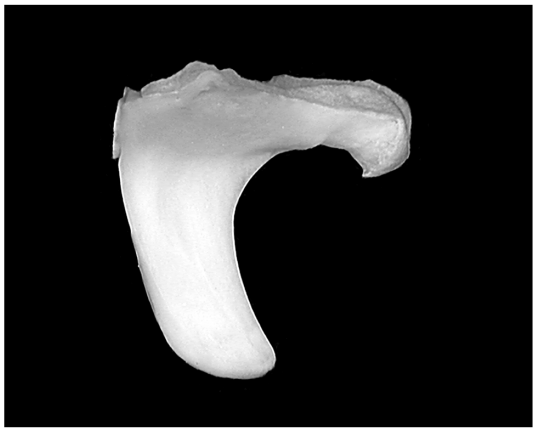
189(0): CJB 490, *ruber* (basioccipital, lateral); concavity absent between ventral and condylar processes.



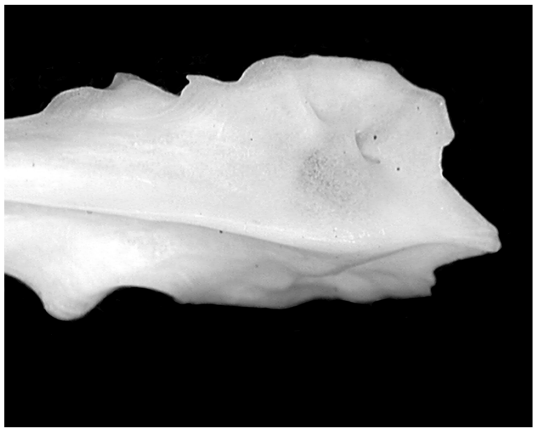
189(1): TJL 930, *polystictus* (basioccipital, lateral); concavity present between ventral and condylar processes.



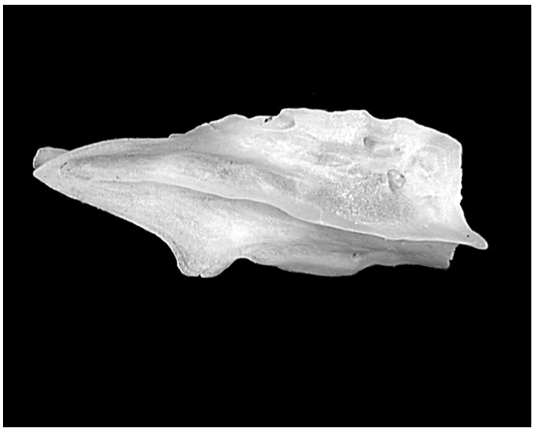
190(0): CJB 693, *mitchellii* (basioccipital, lateral); height of bone less than length of bone.



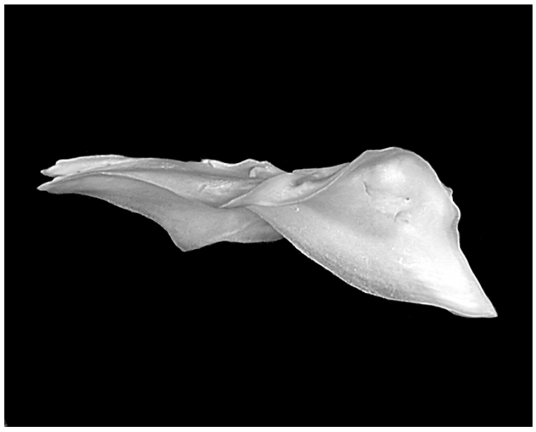
190(1): LSUMZ 22111, *scutulatus* (basi-occipital, lateral); height of bone greater than length of bone.



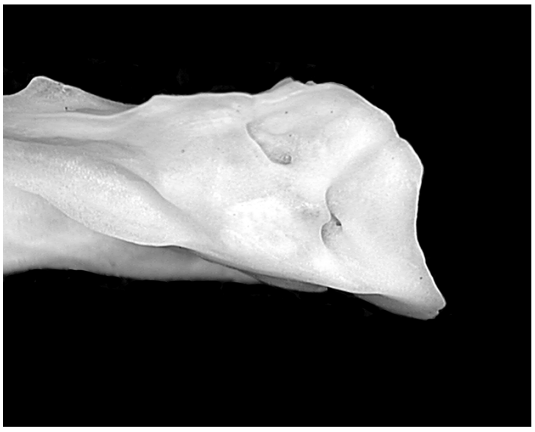
191(0): CJB 699, *cerastes* (sphenoid, ventral); ventral process absent, only elevated or rounded edge or nothing.



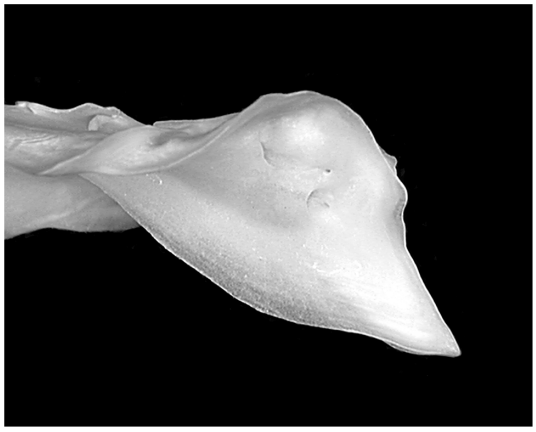
191(1): CJB 1064, *enyo* (sphenoid, ventral); ventral process with low vertical edge.



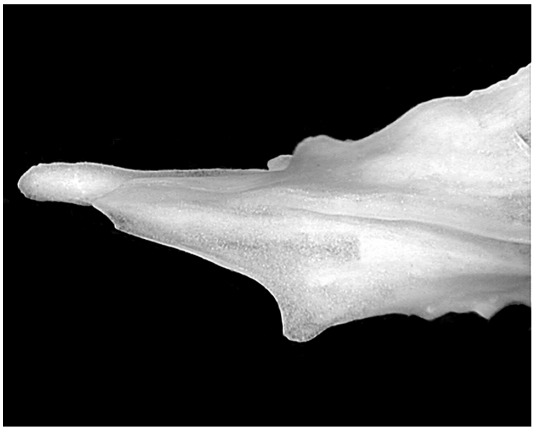
191(2): CJB 001, *atrox* (sphenoid, ventral); ventral process with conspicuous high vertical edge.



192(0): CJB 715, *contortrix* (sphenoid, ventral); elevated ventral process not continuous to posterior edge.



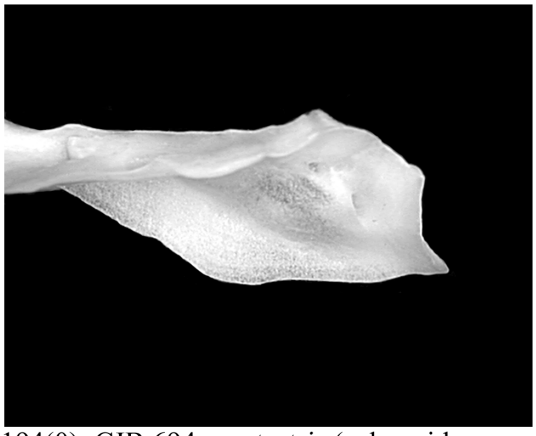
192(1): CJB 001, *atrox* (sphenoid, ventral); elevated ventral process continuous to posterior edge.



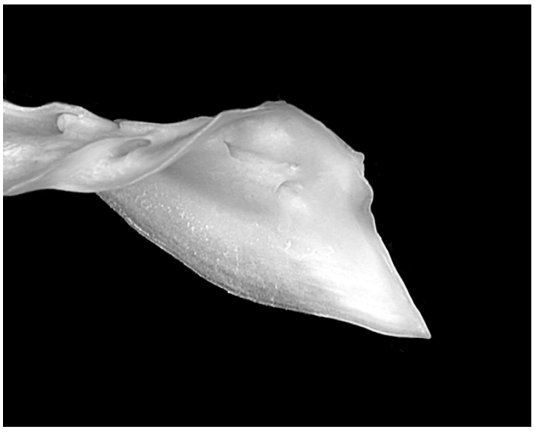
193(0): CJB 691, *catenatus* (sphenoid, ventral); elevated ventral process not continuous to anterior edge.

193(1): CJB 001, *atrox* (sphenoid, ventral); elevated ventral process continuous to anterior edge, but terminates inside concavity.

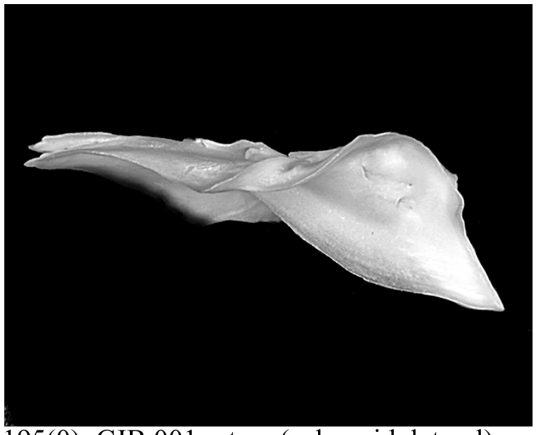
193(2): NAUQSP 14086, *basiliscus* (sphenoid, ventral); elevated ventral process continuous to anterior edge.



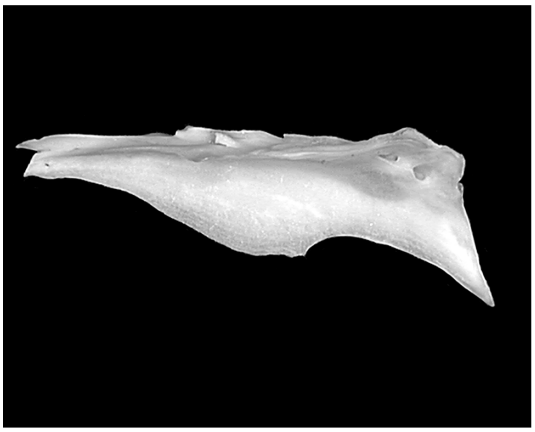
194(0): CJB 694, *contortrix* (sphenoid, lateral); highest peak of ventral process in anterior portion of basisphenoid region.



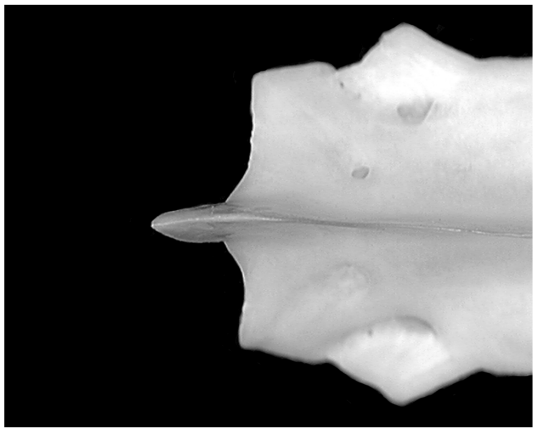
194(1): CJB 001, *atrox* (sphenoid, lateral); highest peak of ventral process in posterior portion of basisphenoid region.



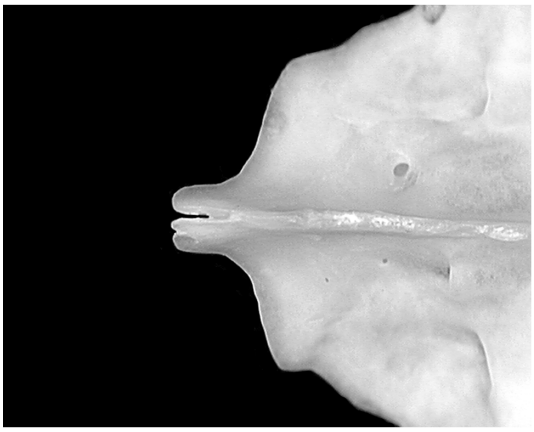
195(0): CJB 001, *atrox* (sphenoid, lateral); only single peak on ventral process.



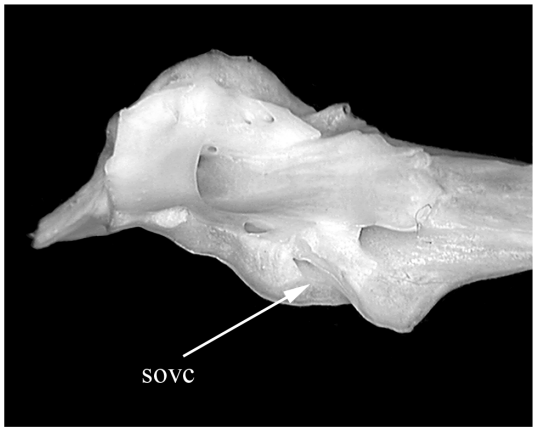
195(1): LSUMZ 29347, *durissus* (sphenoid, lateral); more than one peak on ventral process.



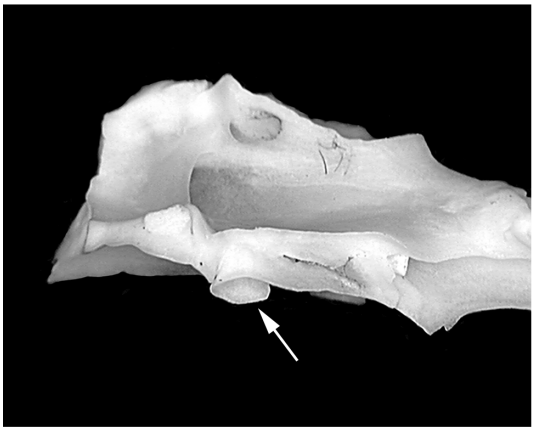
196(0): CJB 697, *molossus* (sphenoid, dorsal); distal point on ventral process not divided.



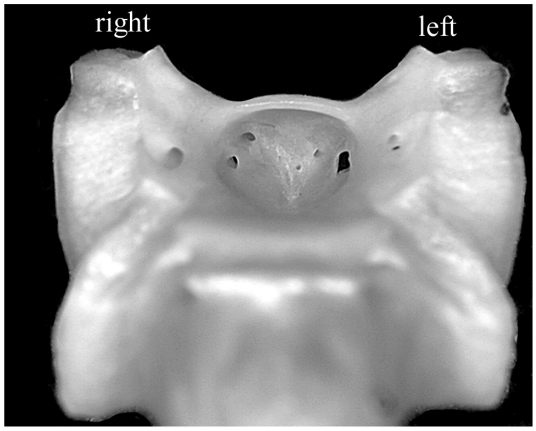
196(1): CJB 577, *atrox* (sphenoid, dorsal); distal point on ventral process divided.



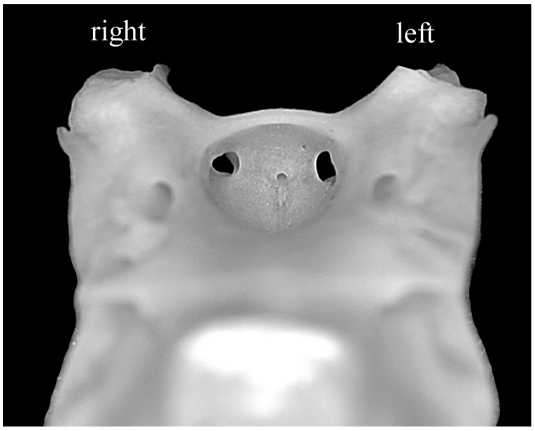
197(0): CJB 001, *atrox* (sphenoid, lateral); absence of small ventrolateral process posterior to secondary ant. vidian opening.



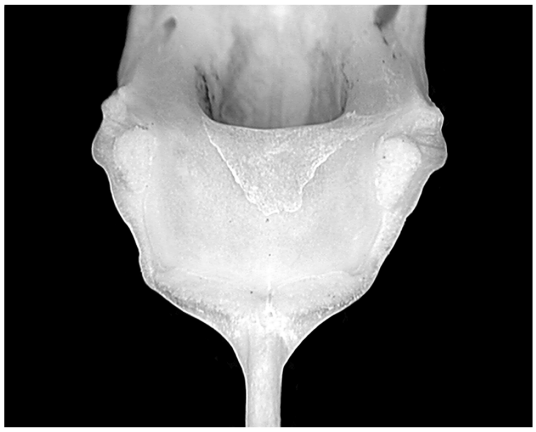
197(1): CJB 508, *piscivorus* (sphenoid, lateral); presence of small ventrolateral process posterior to secondary ant. vidian opening.



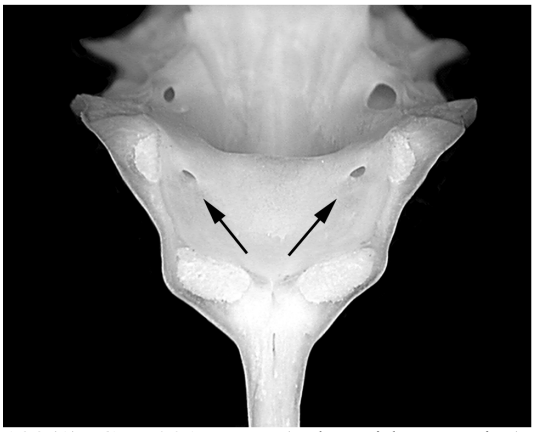
198(0): CJB 001, *atrox* (sphenoid, anterior); pituitary recess, diameter of right side foramen reduced, ~1/2 diameter of left.



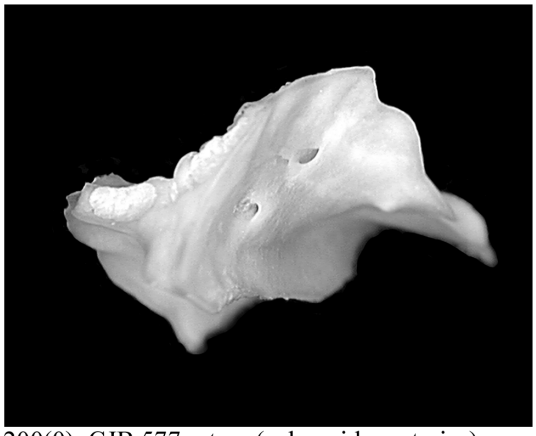
198(1): CJB 490, *ruber* (sphenoid, anterior); pituitary recess, diameter of both left and right foramina roughly equivalent.



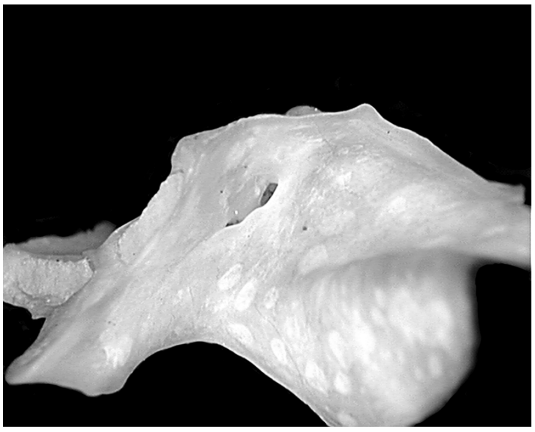
199(0): TJL 930, *polystictus* (sphenoid, posterior); foramina for entrance of abducens nerve absent.



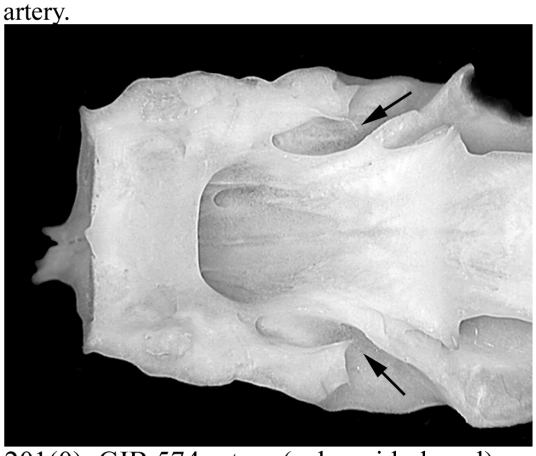
199(1): CJB 001, *atrox* (sphenoid, posterior); foramina for entrance of abducens nerve present.



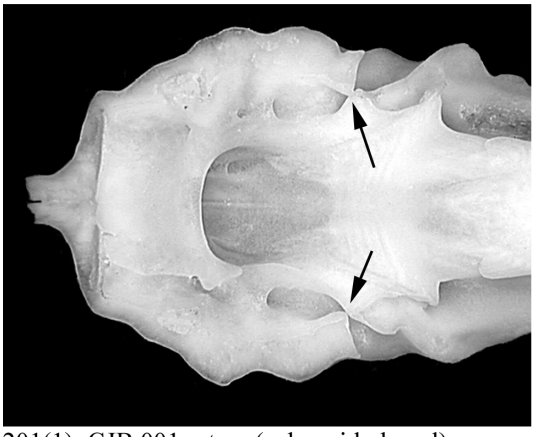
200(0): CJB 577, *atrox* (sphenoid, posterior); separate external foramen for both vidian canal and cerebral branch of internal carotid artery.



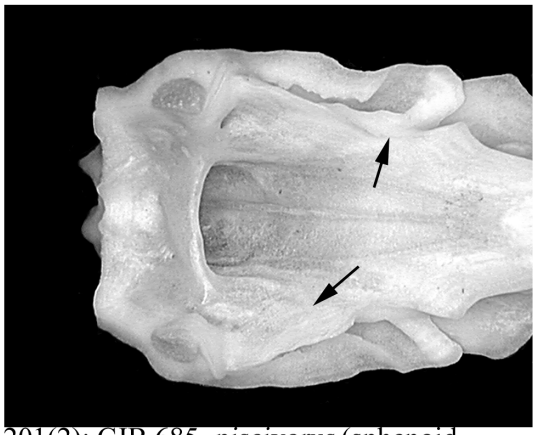
200(1): CJB 149, *bilineatus* (sphenoid, posterior); common external foramen for both vidian canal and cerebral branch of internal carotid artery.



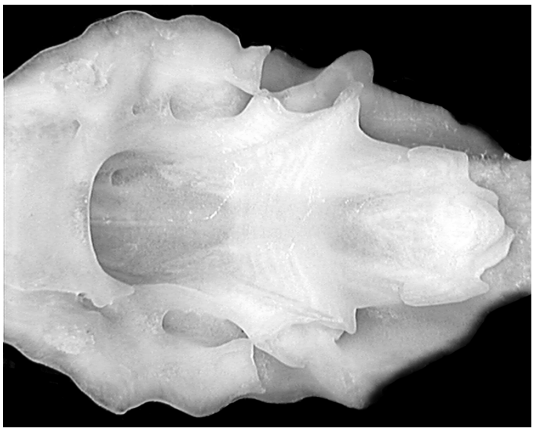
201(0): CJB 574, *atrox* (sphenoid, dorsal); no secondary roof formed in anterior portion of vidian canal, completely open.



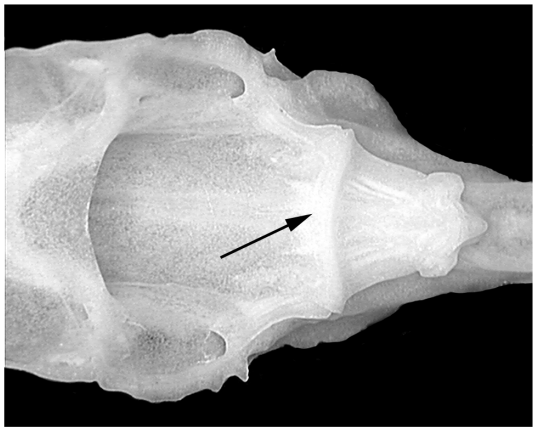
201(1): CJB 001, *atrox* (sphenoid, dorsal); secondary roof formed in anterior portion of vidian canal, forming secondary foramina on at least one side.



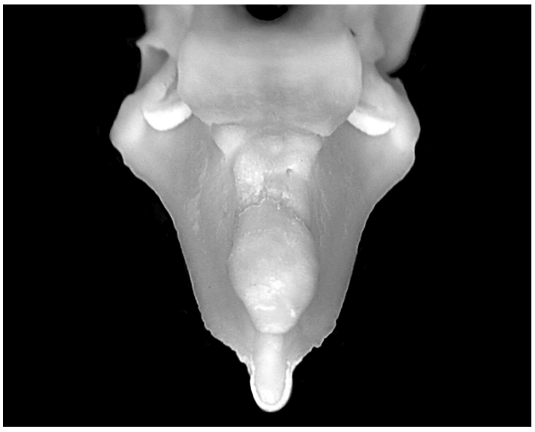
201(2): CJB 685, *piscivorus* (sphenoid, dorsal); anterior portion of vidian canal completely roofed, no secondary foramina.



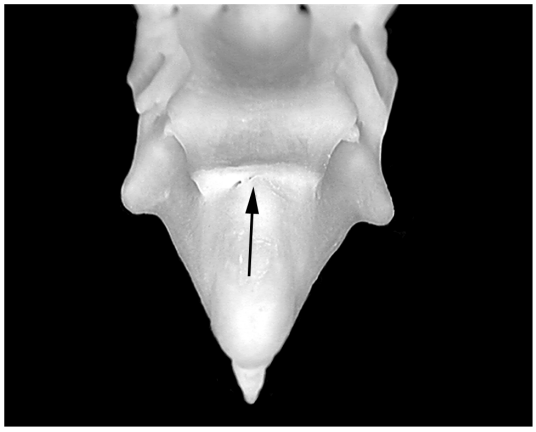
202(0): CJB 577, *atrox* (sphenoid, dorsal); horizontal ridge between anteriormost lateral processes that articulate with parietal absent.



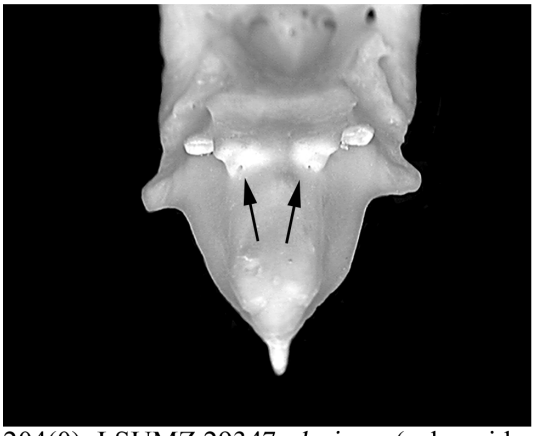
202(1): NAUQSP 7381, *tigris* (sphenoid, dorsal); horizontal ridge between anteriormost lateral processes that articulate with parietal present.



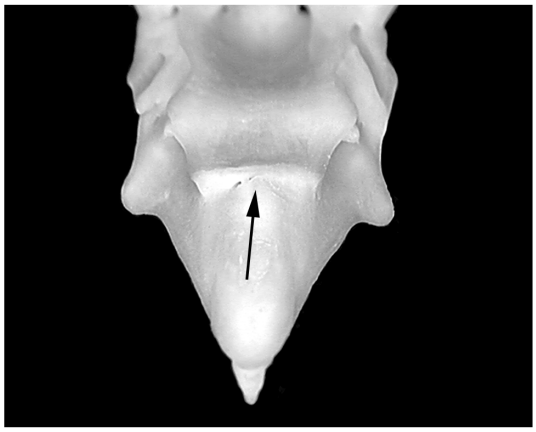
203(0): CJB 705, *piscivorus* (sphenoid, anterodorsal); frontal step of cultiform process absent.



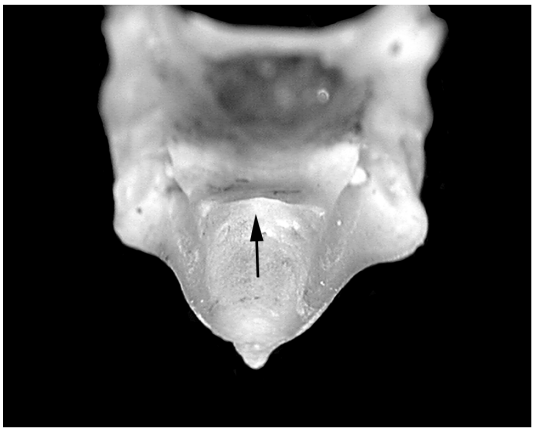
203(1): CJB 697, *molossus* (sphenoid, anterodorsal); frontal step of cultiform process present.



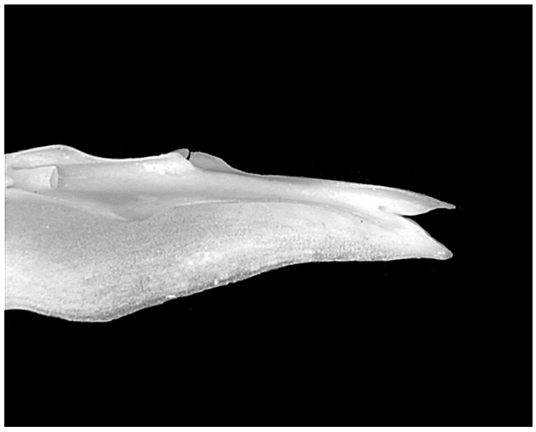
204(0): LSUMZ 29347, *durissus* (sphenoid, anterodorsal); frontal step of cultiform process only present laterally.



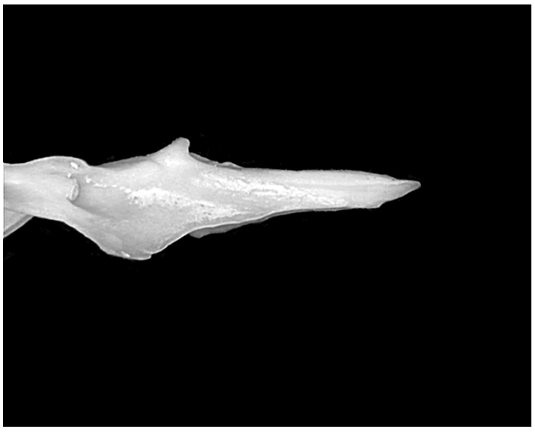
204(1): CJB 697, *molossus* (sphenoid, anterodorsal); frontal step of cultiform process present and entire.



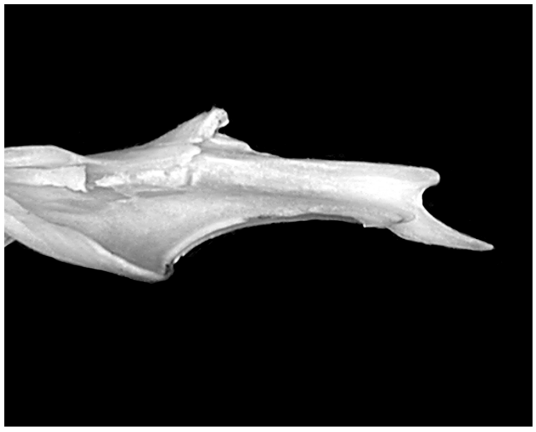
204(2): SDNHM 46949, *catalinensis* (sphenoid, anterodorsal); frontal step of cultiform process only present medially.



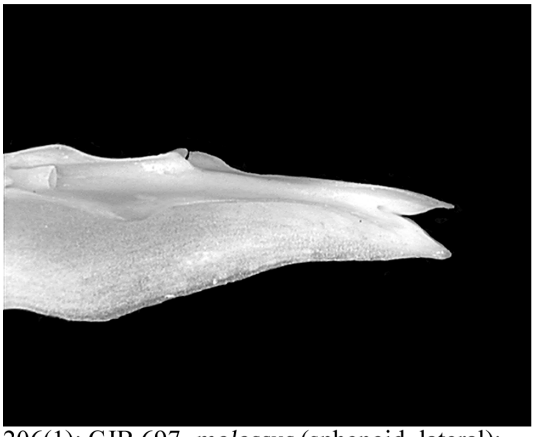
205(0): CJB 697, *molossus* (sphenoid, anterolateral); dorsal and ventral surface of anterior edge of cultiform process separate.



205(1): NAUQSP 7331, *contortrix* (sphenoid, lateral); dorsal and ventral surface of anterior edge of cultiform process fused.

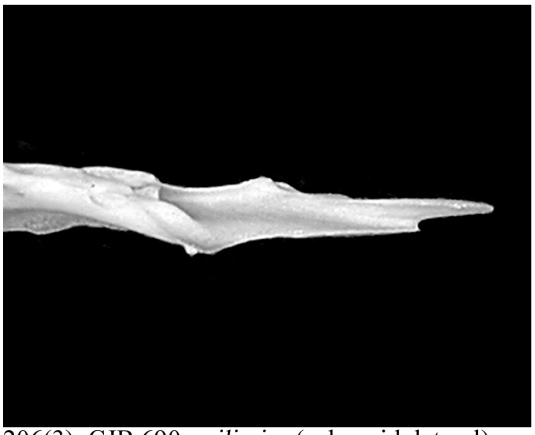


206(0): TJL 930, *polystictus* (sphenoid, lateral); anterior edge of cultiform process, ventral surface extends farther anterior than dorsal surface.

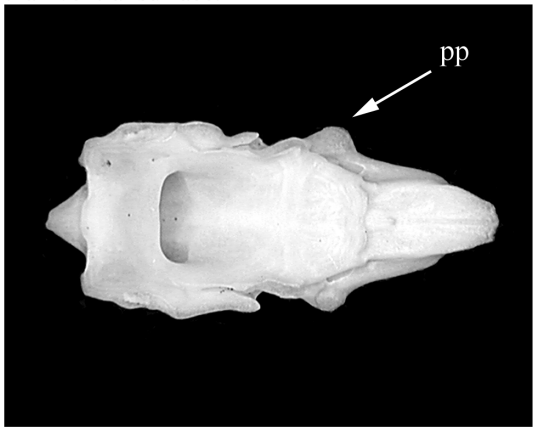


206(1): CJB 697, *molossus* (sphenoid, lateral); anterior edge of cultiform process, dorsal and ventral surface extend roughly equal distance anteriorly.

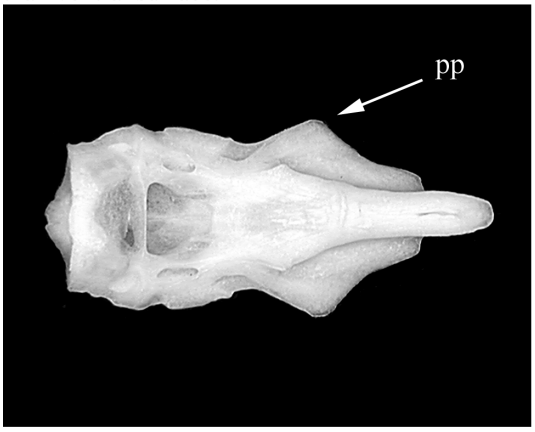
206(2): CJB 490, *ruber* (sphenoid, lateral); anterior edge of cultiform process, dorsal surface extends slightly farther anteriorly than ventral surface.



206(3): CJB 690, *miliarius* (sphenoid, lateral); anterior edge of cultiform process, dorsal surface extends conspicuously farther anteriorly than ventral surface.



207(0): CJB 699, *cerastes* (sphenoid, dorsal); width of pterygoid process does not extend beyond width of basisphenoid region.



207(1): CJB 694, *contortrix* (sphenoid, dorsal); width of pterygoid process does extend beyond width of basisphenoid region.

Appendix F

Complete data matrix used in phylogenetic analyses.

Matrix is separated into three sections: morphology, ND5, 12S/tRNA^{val}/16S data sets.

morphology data set

	1					5								15
adamanteus	P	P	H	S	X	P	H	O	A	B	S	Y	W	c	c
aquilus	E	I	E	N	I	Q	G	P	N	O	?	?	?	?	?
atrox	I	S	D	V	W	R	S	W	G	E	X	M	Y	b	c
basiliscus	M	V	H	U	V	Q	U	S	L	G	S	W	Q	c	c
catalinensi	I	?	?	S	Q	T	?	?	?	?	?	?	?	?	?
catenatus	I	D	G	O	M	Q	Q	Q	M	K	F	H	I	?	a
cerastes	A	D	A	P	N	S	G	T	J	J	G	K	H	c	c
durissus	P	Q	H	T	V	L	X	R	G	D	H	L	R	a	c
enyo	I	M	D	R	P	Q	U	W	N	J	H	U	P	c	c
horridus	E	O	D	R	S	L	S	T	H	E	M	N	P	a	c
intermedius	A	K	D	I	B	V	K	Q	Y	W	A	B	A	a	c
lepidus	E	M	C	O	I	H	K	W	P	O	G	F	F	a	b
miliarius	E	A	J	L	I	Q	G	F	O	O	I	?	E	?	a
mitchellii	I	Q	D	W	T	Q	Y	Y	Q	J	G	J	N	b	c
molossus	M	U	D	Y	Y	P	J	U	B	B	A	N	H	?	c
polystictus	I	N	E	R	Q	U	L	M	C	A	?	?	?	a	c
pricei	A	K	B	G	D	Y	E	P	Q	Q	G	K	I	?	c
pusillus	E	K	I	O	I	T	C	D	F	H	?	?	?	c	c
ravus	A	G	G	M	H	P	D	L	H	J	?	?	?	?	c
ruber	P	W	D	W	Y	S	M	S	E	D	P	K	T	b	c
scutulatus	I	R	D	U	U	S	T	U	L	H	K	J	S	{a,b}	c
stejnegeri	M	Q	Q	U	U	U	K	A	C	B	?	?	?	c	b
tigris	E	N	D	S	P	V	Y	X	S	L	O	M	S	b	c
tortugensis	M	T	B	V	W	S	T	S	I	E	Y	Q	W	b	c
transversus	A	G	D	G	A	T	?	O	X	Y	?	?	?	?	?
triseriatus	E	F	G	O	J	V	A	H	I	J	D	A	G	a	c
unicolor	M	L	G	Q	O	K	M	T	G	F	?	O	Q	a	c
vegrandis	M	O	H	T	S	O	?	?	?	?	?	?	?	?	?
viridis	M	R	E	U	U	V	K	T	J	H	J	Q	Q	a	c
willardi	I	I	F	R	P	K	B	Q	H	J	K	L	C	b	c
bilineatus	E	B	Y	E	G	B	?	?	E	I	?	?	?	?	?
contortrix	E	G	Q	D	C	B	?	?	N	O	?	?	?	?	?
piscivorus	I	B	Q	D	G	A	?	?	H	M	?	?	?	?	?
muta	Y	y	y	D	?	?	?	?	?	?	?	?	?	?	?
blomhoffii	A	E	T	A	F	I	?	?	K	L	?	?	?	?	?

					20										30
adamanteus	y	y	u	a	a	a	y	y	p	e	a	y	y	y	u
aquilus	y	y	y	a	a	a	y	q	y	y	a	y	y	y	y
atrox	y	y	y	a	a	a	y	k	a	p	a	y	y	y	y
basiliscus	y	m	a	a	a	a	y	k	s	y	m	s	s	g	a
catalinensi	y	y	y	a	a	a	y	y	m	?	?	y	y	y	m
catenatus	y	y	u	a	a	a	y	u	u	y	g	y	y	y	y
cerastes	y	y	y	a	a	a	y	e	y	p	a	y	y	y	p
durissus	y	u	a	a	a	a	y	a	m	y	e	y	u	j	j
enyo	y	y	y	a	a	a	y	a	y	q	a	y	y	y	y
horridus	y	y	y	a	a	a	y	a	y	y	a	y	y	u	u
intermedius	y	y	y	a	a	a	?	?	?	?	?	?	?	?	?
lepidus	y	y	y	a	a	a	y	p	y	y	a	y	y	y	y
miliarius	y	y	a	a	a	a	y	y	y	y	a	y	y	y	y
mitchellii	y	y	y	i	a	a	y	y	u	k	a	y	y	u	u
molossus	y	u	a	a	a	a	y	e	y	y	e	u	p	p	p
polystictus	a	a	a	a	a	a	y	a	y	?	?	?	?	?	?
pricei	y	y	y	a	a	a	p	a	e	y	a	y	y	y	y
pusillus	y	y	y	a	a	a	y	y	y	y	a	y	y	y	y
ravus	y	y	m	a	a	a	y	a	y	y	a	y	y	y	y
ruber	y	y	y	a	a	a	y	y	k	u	a	y	y	y	y
scutulatus	y	u	u	e	a	a	y	p	y	u	e	y	u	u	u
stejnegeri	y	y	y	a	a	a	y	y	y	a	a	y	y	y	y
tigris	y	y	y	a	a	a	y	k	e	p	a	y	y	y	u
tortugensis	y	y	y	a	a	a	?	?	a	y	a	y	y	y	y
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	y	y	u	a	a	a	y	a	y	u	e	y	y	y	y
unicolor	y	y	s	a	a	a	y	s	y	y	i	y	y	y	s
vegrandis	y	m	a	a	a	a	?	?	?	y	m	y	a	a	a
viridis	y	y	y	a	a	a	y	y	y	u	a	y	y	y	k
willardi	y	y	m	a	a	a	y	y	y	y	a	y	y	y	y
bilineatus	y	y	y	m	a	a	y	a	y	y	a	y	y	y	y
contortrix	y	y	y	y	y	a	y	a	y	p	a	y	y	y	u
piscivorus	y	y	y	y	y	e	y	u	u	p	a	y	y	y	y
muta	y	y	p	a	a	a	y	m	a	y	a	y	y	y	y
blomhoffii	y	y	y	y	a	a	y	m	e	s	a	y	y	y	y

					35										45
adamanteus	u	a	u	y	a	u	a	a	u	a	a	a	y	u	u
aquilus	g	a	y	y	a	y	a	a	a	a	?	?	m	a	a
atrox	p	a	y	y	a	f	a	a	p	e	a	a	y	y	y
basiliscus	a	a	y	y	a	m	a	a	y	s	m	a	s	m	I
catalinensi	m	a	y	y	a	y	m	m	m	m	y	a	y	m	a
catenatus	u	a	a	?	a	u	y	y	k	e	e	a	y	p	k
cerastes	a	a	f	y	e	y	a	a	k	e	a	a	y	p	y
durissus	j	e	f	y	a	f	e	e	y	u	a	a	y	y	e
enyo	m	a	y	y	a	s	a	a	y	e	a	a	y	u	p
horridus	j	a	k	y	p	a	a	a	u	a	e	a	y	e	y
intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
lepidus	y	u	p	y	a	y	e	a	k	a	s	a	e	a	u
miliarius	y	u	s	y	a	u	y	y	e	a	a	a	p	a	u
mitchellii	m	a	y	u	a	u	a	a	y	i	g	a	y	q	u
molossus	p	a	p	y	a	f	a	a	y	a	k	a	y	u	u
polystictus	?	?	q	m	a	y	y	a	q	i	a	a	m	i	a
pricei	u	a	q	y	a	y	a	a	e	a	y	a	a	a	p
pusillus	y	y	y	y	a	a	a	a	y	a	?	?	a	a	a
ravus	y	a	a	?	a	m	a	a	y	a	?	?	y	m	a
ruber	u	a	y	y	a	a	a	a	u	e	a	a	y	y	y
scutulatus	j	a	y	y	a	p	a	a	p	a	a	a	y	a	u
stejnegeri	y	y	a	?	a	y	a	a	a	a	?	?	y	y	a
tigris	j	a	y	y	a	p	a	a	u	a	a	a	m	a	k
tortugensis	m	a	m	y	a	m	a	a	y	m	?	?	y	y	?
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	y	k	y	y	a	u	k	e	u	a	?	?	a	a	a
unicolor	m	a	y	y	a	y	a	a	y	a	y	a	y	m	y
vegrandis	a	a	y	y	a	a	a	a	y	m	?	?	y	m	m
viridis	e	a	y	y	a	a	a	a	y	y	a	a	y	u	y
willardi	y	a	y	y	a	s	a	a	g	a	y	a	g	g	y
bilineatus	a	a	y	y	a	y	a	a	m	a	y	a	y	y	y
contortrix	a	a	u	y	a	y	a	a	y	a	a	a	u	p	y
piscivorus	p	e	y	k	a	u	a	a	y	e	y	a	e	e	u
muta	y	m	y	s	a	y	u	a	e	a	y	m	k	a	i
blomhoffii	a	a	y	a	a	s	a	a	g	a	y	a	g	a	y

					50										60
adamanteus	e	a	b	y	y	s	s	a	a	a	a	a	a	a	a
aquilus	a	?	d	m	s	g	g	a	a	a	a	a	a	a	a
atrox	u	a	d	y	u	u	u	j	a	a	a	a	a	a	a
basiliscus	a	a	d	y	y	y	y	s	a	a	a	a	a	a	a
catalinensi	a	a	d	?	y	y	y	m	a	a	a	a	a	a	a
catenatus	a	a	d	y	y	a	a	a	a	a	a	a	a	a	a
cerastes	y	a	d	y	u	u	u	p	e	a	a	a	a	a	a
durissus	e	a	d	y	y	y	y	e	a	a	a	a	a	a	a
enyo	e	a	d	y	y	y	e	a	a	a	a	a	a	a	a
horridus	u	a	d	y	y	y	y	y	k	e	a	a	a	a	a
intermedius	?	?	?	?	a	a	a	a	a	a	a	a	a	a	a
lepidus	e	a	d	f	y	y	e	a	a	a	a	a	a	a	a
miliarius	e	a	d	y	y	u	e	a	a	a	a	a	a	a	a
mitchellii	i	a	d	u	y	y	u	e	a	a	a	a	a	a	a
molossus	e	a	d	y	y	y	y	e	a	a	a	a	a	a	a
Polystictus	a	a	{b,c}	y	y	a	a	a	a	a	a	a	a	a	a
pricei	a	a	d	k	y	i	a	a	a	a	a	a	a	a	a
pusillus	a	a	d	y	y	y	y	a	a	a	a	a	a	a	a
ravus	a	a	d	m	y	y	y	m	a	a	a	a	a	a	a
ruber	y	a	{b,d}	y	y	y	u	a	a	a	a	a	a	a	a
scutulatus	a	a	d	y	y	y	p	a	a	a	a	a	a	a	a
stejnegeri	a	a	d	y	y	y	a	a	a	a	a	a	a	a	a
tigris	k	a	d	y	y	y	y	e	a	a	a	a	a	a	a
tortugensis	?	a	d	y	y	y	y	m	a	a	a	a	a	a	a
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	a	a	d	y	y	u	e	a	a	a	a	a	a	a	a
unicolor	a	a	d	y	m	m	g	a	a	a	a	a	a	a	a
vegrandis	a	a	{b,d}	y	y	y	a	a	a	a	a	a	a	a	a
viridis	p	a	d	y	y	u	j	a	a	a	a	a	a	a	a
willardi	m	a	{b,c}	q	y	a	a	a	a	a	a	a	a	a	a
bilineatus	m	b	d	a	y	y	y	y	y	y	y	y	y	y	p
contortrix	p	b	d	a	y	y	y	y	y	y	y	y	y	u	u
piscivorus	u	b	d	a	y	y	y	y	y	y	y	y	m	m	m
muta	a	b	d	y	y	y	y	y	u	a	a	a	a	a	a
blomhoffii	a	a	d	a	y	y	y	y	y	s	s	m	a	a	a

					65										75
adamanteus	a	a	y	a	y	p	a	b	k	q	k	y	a	y	p
aquilus	a	a	m	a	a	?	?	b	a	g	g	y	a	y	I
atrox	a	a	y	a	a	a	a	b	k	a	u	s	a	y	k
basiliscus	a	a	y	a	a	a	a	b	a	g	m	y	a	y	s
catalinensi	a	a	y	a	y	a	a	b	a	y	y	y	a	y	a
catenatus	a	a	q	a	y	a	a	b	f	f	k	y	a	y	u
cerastes	a	a	y	a	a	a	a	b	k	a	a	?	?	p	a
durissus	a	a	y	a	a	y	a	b	f	a	g	y	a	y	g
enyo	a	a	y	a	a	a	a	b	a	a	a	?	?	y	y
horridus	a	a	y	e	a	k	a	b	y	a	u	s	a	u	j
intermedius	a	a	?	?	?	?	?	?	?	?	?	?	?	?	?
lepidus	a	a	y	a	a	a	a	b	m	a	a	?	?	y	k
miliarius	a	a	y	a	a	a	a	b	g	p	a	?	?	y	a
mitchellii	a	a	y	a	a	m	a	b	m	e	e	y	a	y	y
molossus	a	a	y	a	a	a	a	b	a	p	y	y	a	y	y
polystictus	a	a	y	a	u	a	a	b	i	a	q	y	g	y	i
pricei	a	a	y	a	a	a	a	b	a	a	a	?	?	y	e
pusillus	a	a	y	a	a	a	a	b	a	a	a	?	?	y	y
ravus	a	a	y	a	a	a	a	b	a	a	a	?	?	y	y
ruber	a	a	y	a	a	a	a	b	a	f	u	y	a	y	y
scutulatus	a	a	y	a	a	a	a	b	k	f	p	y	a	y	y
stejnegeri	a	a	y	a	a	a	a	b	a	?	a	?	?	y	y
tigris	a	a	y	a	k	a	a	b	a	f	a	?	?	y	y
tortugensis	a	a	y	a	a	?	?	b	a	a	a	?	?	y	y
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	a	a	s	a	m	a	a	b	a	a	u	y	a	y	a
unicolor	a	a	y	a	a	a	a	b	a	a	i	y	a	q	a
vegrandis	a	a	y	a	a	?	?	b	a	a	a	?	?	y	m
viridis	a	a	y	a	a	a	a	b	p	p	k	y	a	y	u
willardi	a	a	q	a	a	a	a	b	a	g	m	y	a	y	a
bilineatus	j	e	y	y	a	y	y	b	a	a	a	?	?	y	y
contortrix	j	a	y	y	a	y	y	b	a	a	a	?	?	y	a
piscivorus	m	m	y	y	a	y	y	b	a	f	f	a	a	y	u
muta	a	a	y	a	a	y	a	b	a	a	a	?	?	y	y
blomhoffii	a	a	y	q	a	y	a	b	a	a	i	y	a	y	m

					80										90
adamanteus	y	y	u	y	u	y	a	y	y	y	e	a	a	a	a
aquilus	m	a	y	a	y	y	a	y	m	a	a	a	a	a	a
atrox	y	y	y	f	u	y	a	y	u	u	p	a	a	a	a
basiliscus	y	y	y	m	q	y	a	y	y	y	a	a	a	a	a
catalinensi	y	y	y	y	y	y	a	y	y	y	a	a	a	a	a
catenatus	u	k	p	f	y	y	a	y	y	e	e	a	a	a	a
cerastes	f	u	u	a	k	y	a	u	u	e	a	a	a	a	a
durissus	y	y	y	s	m	y	a	y	u	e	a	a	a	a	a
enyo	y	y	y	g	y	y	a	y	y	a	a	a	a	a	a
horridus	p	u	y	a	u	y	a	y	y	y	y	e	a	a	a
intermedius	?	?	?	?	?	?	?	y	a	a	a	a	a	a	a
lepidus	f	p	y	a	k	y	a	y	e	a	a	a	a	a	a
miliarius	f	u	y	a	y	y	a	y	y	y	u	a	a	a	a
mitchellii	y	p	y	k	y	y	a	y	u	e	a	a	a	a	a
molossus	y	y	y	g	m	y	a	y	y	u	a	a	a	a	a
polystictus	m	i	y	u	y	y	a	y	e	a	a	a	a	a	a
pricei	u	p	y	f	a	y	y	y	u	a	a	a	a	a	a
pusillus	y	y	y	y	y	y	a	y	y	y	a	a	a	a	a
ravus	y	a	y	a	y	y	a	y	y	m	a	a	a	a	a
ruber	y	y	y	a	p	y	a	y	y	p	a	a	a	a	a
scutulatus	u	u	y	k	p	y	a	y	y	y	e	a	a	a	a
stejnegeri	y	y	y	y	a	y	a	y	y	y	a	a	a	a	a
tigris	y	y	y	a	g	y	a	y	a	a	a	a	a	a	a
tortugensis	y	y	m	y	m	y	a	y	y	y	a	a	a	a	a
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	y	s	y	f	y	y	a	y	u	e	e	a	a	a	a
unicolor	y	y	y	q	a	y	a	y	a	a	a	a	a	a	a
vegrandis	y	y	y	y	y	y	a	y	y	a	a	a	a	a	a
viridis	u	u	y	a	u	y	a	y	u	j	a	a	a	a	a
willardi	y	m	y	a	g	y	a	q	a	a	a	a	a	a	a
bilineatus	y	m	y	a	a	y	m	y	y	y	y	y	m	m	m
contortrix	y	f	y	a	a	y	k	y	y	y	y	y	y	u	u
piscivorus	y	a	y	a	a	u	a	y	y	y	y	y	y	y	y
muta	y	y	y	u	y	u	a	y	y	y	i	e	e	a	a
blomhoffii	y	a	y	a	g	a	?	y	y	y	y	m	a	a	a

					95										105
adamanteus	a	a	a	y	u	a	a	a	a	a	a	y	p	u	a
aquilus	a	a	a	m	a	a	s	g	a	a	a	s	a	g	m
atrox	a	a	a	y	y	a	k	e	a	a	a	m	a	s	a
basiliscus	a	a	a	y	m	a	a	a	a	s	s	m	a	y	a
catalinensi	a	a	a	y	y	a	m	a	a	a	a	y	a	a	m
catenatus	a	a	a	a	?	a	p	j	a	y	y	p	e	?	a
cerastes	a	a	a	k	y	a	p	j	a	e	e	s	g	i	g
durissus	a	a	a	y	f	a	a	a	a	y	y	m	a	?	a
enyo	a	a	a	y	u	a	e	e	a	a	a	y	a	u	a
horridus	a	a	a	y	p	a	y	y	a	a	a	y	i	i	a
intermedius	a	a	a	?	?	?	?	?	?	?	?	?	?	?	?
lepidus	a	a	a	k	m	a	k	a	a	a	a	u	a	k	a
miliarius	a	a	a	f	y	a	k	a	a	y	y	p	e	?	a
mitchellii	a	a	a	y	y	a	a	a	a	a	a	a	a	m	a
molossus	a	a	a	y	y	a	a	a	a	y	y	k	a	?	a
polystictus	a	a	a	y	y	a	y	u	a	a	a	q	a	i	a
pricei	a	a	a	p	a	a	k	a	a	a	a	k	a	g	a
pusillus	a	a	a	a	?	a	a	a	a	a	a	a	a	a	a
ravus	a	a	a	m	y	a	y	m	a	y	y	m	a	?	a
ruber	a	a	a	y	k	a	y	y	a	k	e	y	e	s	a
scutulatus	a	a	a	y	p	a	e	a	f	e	e	i	a	a	a
stejnegeri	a	a	a	a	?	a	y	a	a	y	a	y	a	a	a
tigris	a	a	a	y	k	a	a	a	e	a	a	k	e	s	a
tortugensis	a	a	a	y	y	a	y	m	a	y	m	a	a	?	a
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	a	a	a	g	a	a	y	a	k	p	j	u	a	y	a
unicolor	a	a	a	y	s	a	a	a	a	y	y	a	a	?	a
vegrandis	a	a	a	y	y	a	a	a	a	y	y	a	a	?	a
viridis	a	a	a	y	f	a	a	a	f	a	a	g	a	g	a
willardi	a	a	a	y	y	a	y	m	a	a	a	a	a	g	a
bilineatus	m	m	a	a	?	b	a	a	y	a	a	a	a	y	a
contortrix	e	e	e	a	?	a	a	a	y	a	a	y	e	y	a
piscivorus	y	y	u	a	?	b	a	a	y	a	a	a	a	y	a
muta	a	a	a	e	a	a	a	a	y	a	a	u	e	q	y
blomhoffii	a	a	a	a	?	a	a	a	i	a	a	s	m	y	y

					110										120
adamanteus	k	a	a	y	k	e	a	p	a	y	u	u	p	a	y
aquilus	m	a	a	q	a	a	a	y	g	a	y	a	a	a	y
atrox	p	a	f	y	e	a	a	y	y	a	y	e	a	a	y
basiliscus	s	a	g	y	y	y	a	a	a	a	y	m	g	a	y
catalinensi	m	a	a	m	a	a	a	y	y	a	m	a	a	a	m
catenatus	a	a	a	y	y	u	a	y	k	a	y	k	a	a	y
cerastes	f	a	a	y	p	e	a	y	k	a	p	k	a	a	y
durissus	y	a	a	y	s	s	a	k	a	k	p	p	a	a	y
enyo	u	a	g	y	e	e	a	u	k	f	y	u	a	a	y
horridus	y	a	a	y	k	e	a	u	p	a	y	u	a	a	y
intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
lepidus	p	a	f	u	a	a	a	p	f	a	y	k	a	a	y
miliarius	f	a	f	y	e	e	a	p	f	f	p	e	a	a	y
mitchellii	u	a	e	y	m	m	a	i	e	i	y	y	a	a	y
molossus	u	a	a	y	u	u	a	a	a	y	u	u	j	a	y
polystictus	q	a	a	y	e	e	a	q	a	i	m	a	a	a	y
pricei	a	a	a	y	e	e	a	y	k	k	k	a	a	a	y
pusillus	a	a	a	y	a	a	a	y	a	y	y	a	a	a	y
ravus	a	a	a	y	a	a	a	m	m	m	m	a	a	a	y
ruber	u	a	f	y	k	k	a	y	p	a	p	k	a	a	y
scutulatus	y	a	f	y	u	u	a	y	a	a	p	k	e	a	y
stejnegeri	a	a	a	a	?	?	a	a	a	a	y	a	a	a	y
tigris	y	a	a	y	k	k	a	a	a	k	f	e	a	a	y
tortugensis	y	a	a	y	m	m	a	y	m	a	y	a	a	m	y
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	k	a	a	k	a	a	a	u	f	k	y	p	a	a	y
unicolor	y	a	a	s	a	a	a	g	g	y	y	a	a	a	y
vegrandis	y	a	a	y	a	a	a	y	a	y	y	m	m	a	y
viridis	k	a	a	u	y	s	a	p	u	p	p	u	a	a	y
willardi	g	a	g	m	m	a	a	a	g	a	s	q	a	a	y
bilineatus	y	a	a	y	y	m	a	a	a	m	s	a	a	m	y
contortrix	u	a	a	y	k	e	a	a	a	k	y	p	a	a	u
piscivorus	y	a	a	y	y	p	a	p	f	p	p	s	a	a	y
muta	y	a	e	y	u	u	a	y	u	f	p	y	a	a	y
blomhoffii	a	a	a	s	a	a	a	m	s	a	g	a	a	g	y

					125										135
adamanteus	y	a	y	y	a	y	y	a	y	a	a	y	a	g	g
aquilus	m	a	g	s	m	y	g	g	a	a	y	y	a	y	y
atrox	f	c	u	u	a	y	y	a	y	f	a	y	a	g	a
basiliscus	y	a	y	y	a	y	y	a	q	a	m	y	a	k	k
catalinensi	a	a	y	m	m	y	y	a	a	a	y	y	a	a	a
catenatus	u	a	k	k	k	y	p	a	f	a	u	y	a	y	k
cerastes	f	a	p	a	a	y	a	a	a	a	u	y	i	q	I
durissus	y	a	y	u	a	y	y	a	u	a	a	g	a	m	m
enyo	y	a	y	u	p	y	y	a	a	a	y	y	e	y	g
horridus	y	a	u	p	f	y	y	a	k	a	p	y	a	g	a
intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
lepidus	u	a	f	u	u	y	e	a	a	a	y	u	a	y	k
miliarius	k	a	k	u	a	y	a	a	a	a	y	y	g	y	s
mitchellii	u	a	u	q	a	y	u	e	q	a	s	y	a	y	p
molossus	y	a	y	y	a	y	y	a	a	a	y	y	a	y	i
polystictus	a	a	y	u	u	y	u	e	q	a	m	y	a	y	u
pricei	a	a	k	p	p	y	a	a	k	a	y	y	p	p	j
pusillus	y	a	y	y	y	y	y	a	a	a	?	y	a	a	a
ravus	m	a	y	y	y	y	a	a	a	a	y	y	m	y	a
ruber	y	a	y	y	a	y	y	a	y	a	a	y	a	i	a
scutulatus	y	a	u	y	a	y	p	a	a	a	p	u	a	p	a
stejnegeri	a	a	?	a	a	y	a	a	a	a	?	y	a	y	a
tigris	u	a	a	a	a	y	a	a	a	a	q	y	a	q	q
tortugensis	y	a	a	m	a	y	y	a	a	y	?	y	a	y	a
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	y	a	k	y	u	y	p	a	a	a	y	y	e	y	y
unicolor	y	b	s	s	a	y	y	a	y	a	a	y	a	a	a
vegrandis	y	a	y	y	a	y	y	a	y	a	?	y	a	?	?
viridis	y	a	y	u	a	y	u	a	a	a	p	y	k	p	a
willardi	m	a	m	m	g	y	m	a	i	a	y	y	g	y	y
bilineatus	a	a	m	y	a	y	a	a	a	a	y	y	a	a	a
contortrix	a	a	p	y	f	p	a	a	a	a	y	y	u	a	a
piscivorus	a	a	a	u	a	y	a	a	a	a	y	y	s	a	a
muta	f	a	u	k	u	y	k	a	g	a	y	y	a	y	y
blomhoffii	a	a	y	y	s	y	m	a	a	a	y	y	i	y	a

					140										150
adamanteus	m	s	y	a	y	y	a	y	a	a	m	y	k	a	k
aquilus	a	a	m	b	y	a	y	y	a	a	s	y	k	a	y
atrox	g	a	y	a	y	g	y	s	a	a	m	y	g	a	g
basiliscus	m	a	y	b	y	q	y	k	a	a	a	s	m	a	m
catalinensi	y	a	y	a	y	y	y	a	a	a	y	y	y	a	y
catenatus	k	a	y	b	y	e	y	p	y	f	y	y	y	a	p
cerastes	i	a	y	a	y	q	y	y	i	g	q	y	y	f	y
durissus	a	a	y	b	y	y	y	y	a	f	i	y	y	a	u
enyo	y	a	y	b	y	y	y	s	a	a	q	y	f	p	e
horridus	m	a	y	c	y	y	y	m	a	a	m	y	y	f	e
intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
lepidus	u	k	y	b	y	y	y	y	a	a	k	y	y	a	g
miliarius	s	a	y	a	y	y	y	y	a	a	s	u	u	a	k
mitchellii	k	a	y	b	y	s	y	k	a	a	a	u	k	y	i
molossus	y	a	y	b	y	y	y	q	a	a	i	y	y	p	y
polystictus	p	a	g	b	s	m	s	y	a	a	u	y	f	a	p
pricei	k	a	y	b	y	k	y	p	g	a	s	u	p	g	e
pusillus	a	y	?	?	?	?	y	a	y	y	y	y	y	a	y
ravus	y	a	y	a	y	y	y	y	a	a	m	y	y	a	y
ruber	i	a	y	b	y	a	q	y	a	a	a	y	a	g	e
scutulatus	m	a	s	b	y	y	y	s	a	a	p	u	f	a	k
stejnegeri	y	y	?	?	?	?	?	?	y	a	a	a	y	y	y
tigris	q	a	y	c	y	q	y	i	a	a	m	y	y	a	y
tortugensis	a	a	y	b	y	y	a	y	a	a	y	y	a	a	?
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	m	f	y	b	y	m	s	u	a	p	i	y	p	a	u
unicolor	a	a	m	b	m	a	y	y	a	a	a	m	y	a	y
vegrandis	?	a	?	?	?	?	?	m	a	a	a	y	y	a	y
viridis	u	a	y	{b,c}	y	y	y	k	a	a	a	y	u	k	u
willardi	s	a	y	a	y	y	y	a	a	g	i	y	y	q	a
bilineatus	a	a	y	b	y	m	y	m	m	y	m	a	y	a	y
contortrix	k	a	a	?	a	a	y	y	p	y	y	a	y	a	y
piscivorus	s	a	y	b	y	g	y	y	m	s	y	u	y	a	y
muta	y	a	y	b	y	y	y	y	a	a	y	y	y	a	y
blomhoffii	a	a	y	b	y	y	y	y	y	g	y	y	y	a	q

					155										165
adamanteus	p	a	p	a	y	a	y	y	a	f	a	y	y	y	y
aquilus	a	a	?	?	y	?	?	?	m	y	?	a	y	?	?
atrox	y	a	a	a	y	a	p	y	a	a	a	y	y	y	y
basiliscus	s	m	m	a	y	a	a	s	a	s	a	y	y	y	y
catalinensi	y	a	a	a	y	a	a	y	a	y	a	y	y	y	y
catenatus	k	e	y	a	y	a	a	y	y	y	a	a	y	y	y
cerastes	a	a	y	a	y	a	u	a	k	p	a	a	y	y	y
durissus	s	a	a	a	p	a	a	k	a	s	f	y	u	y	y
enyo	m	g	m	a	y	a	m	m	a	y	f	q	y	y	y
horridus	e	a	u	j	y	a	f	k	a	y	a	y	y	y	y
intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
lepidus	g	g	y	a	y	p	y	k	p	p	g	g	y	y	u
miliarius	m	a	y	a	y	a	f	y	u	y	a	g	y	y	y
mitchellii	e	a	s	a	i	a	a	m	a	m	f	u	y	y	y
molossus	p	j	e	a	y	a	a	u	a	u	f	y	y	y	y
polystictus	q	i	y	a	y	e	m	a	a	a	a	q	y	y	y
pricei	p	a	q	i	y	a	u	y	f	y	a	f	u	y	y
pusillus	a	a	a	a	?	?	?	a	a	y	a	y	y	y	y
ravus	y	a	?	?	y	a	?	y	a	y	a	a	y	y	y
ruber	y	u	p	e	y	a	k	y	a	u	a	y	y	y	y
scutulatus	y	p	e	e	y	a	p	y	a	y	a	y	y	y	y
stejnegeri	?	?	?	?	y	?	?	?	a	a	a	?	y	y	y
tigris	y	m	i	a	y	a	u	y	f	y	a	u	y	y	y
tortugensis	?	?	?	?	?	a	?	y	a	y	?	?	y	y	y
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	y	y	?	?	q	a	?	a	a	a	a	i	y	y	y
unicolor	y	a	a	a	y	a	a	a	a	a	a	y	y	y	y
vegrandis	m	a	?	?	?	?	?	y	a	y	?	?	y	y	y
viridis	u	p	p	a	y	k	f	f	f	y	a	a	y	y	y
willardi	m	m	a	a	y	a	y	a	a	y	a	a	y	s	y
bilineatus	y	a	a	a	y	a	a	a	a	y	a	y	y	a	a
contortrix	u	e	a	a	u	a	y	a	p	y	a	f	y	a	a
piscivorus	p	a	k	e	y	a	a	g	a	s	g	m	y	y	k
muta	m	a	?	?	y	?	?	q	a	q	a	?	y	y	y
blomhoffii	y	a	y	a	y	a	y	y	a	y	a	a	y	a	y

					170										180
adamanteus	a	y	y	y	k	u	a	y	y	y	f	y	e	y	y
aquilus	?	?	?	a	m	i	a	y	m	y	a	a	a	a	s
atrox	a	y	y	y	y	i	a	y	y	y	a	y	e	y	y
basiliscus	a	y	y	y	a	y	a	y	y	y	i	s	a	y	y
catalinensi	a	a	y	y	y	y	y	y	y	y	a	m	m	a	y
catenatus	p	a	y	f	y	a	a	y	y	y	a	p	j	u	p
cerastes	a	a	y	a	f	p	a	y	y	p	a	k	a	u	f
durissus	a	a	y	g	y	m	g	y	y	y	a	u	j	y	u
enyo	f	f	y	a	y	g	a	y	p	f	a	e	a	a	f
horridus	u	u	y	y	p	a	a	y	y	u	a	p	j	y	k
intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
lepidus	u	u	y	y	p	a	a	u	y	y	a	u	p	p	k
miliarius	g	g	y	a	a	a	a	y	p	p	a	p	j	k	y
mitchellii	a	m	y	m	y	u	e	u	y	u	a	m	a	u	y
molossus	f	y	y	s	a	a	a	u	y	y	a	u	a	y	y
polystictus	a	a	y	a	a	a	a	y	u	y	a	y	a	u	y
pricei	a	k	y	a	u	a	a	k	y	y	a	y	y	a	p
pusillus	a	a	y	a	a	a	a	y	y	y	a	a	a	a	y
ravus	a	m	y	?	a	a	a	y	m	y	a	a	a	a	m
ruber	a	f	y	y	y	y	a	u	y	u	a	p	a	y	y
scutulatus	a	f	y	p	y	a	a	u	y	u	a	k	a	y	y
stejnegeri	a	a	y	?	y	a	a	y	a	y	a	y	a	y	a
tigris	a	a	y	i	y	a	a	y	y	f	a	a	a	y	y
tortugensis	a	a	y	y	y	a	a	y	y	y	a	y	a	y	y
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	a	a	y	?	q	a	a	y	y	y	a	u	p	a	f
unicolor	a	a	y	m	a	q	a	y	s	s	a	y	m	s	g
vegrandis	a	a	y	?	a	y	a	y	m	y	a	y	m	m	a
viridis	a	a	y	k	y	a	a	y	y	k	a	u	a	y	y
willardi	a	a	y	q	s	a	a	y	y	y	a	i	a	s	g
bilineatus	?	m	y	y	a	a	a	a	y	y	y	y	y	a	m
contortrix	?	a	y	f	y	a	a	p	y	k	f	y	y	a	y
piscivorus	a	f	y	a	f	a	a	f	u	u	y	y	y	a	p
muta	a	y	y	y	s	a	a	u	y	y	a	y	y	a	u
blomhoffii	a	a	m	a	y	a	a	m	y	y	a	m	m	a	f

					185										195
adamanteus	y	f	a	y	a	k	a	a	a	a	a	a	a	a	a
aquilus	y	y	a	y	a	y	y	y	y	y	y	s	s	s	s
atrox	y	u	a	y	a	y	p	e	e	e	e	e	e	e	e
basiliscus	y	a	?	y	a	y	s	a	a	a	a	a	a	a	a
catalinensi	a	y	a	y	a	y	y	y	y	y	m	a	a	a	a
catenatus	p	u	c	y	a	y	y	y	y	u	p	e	e	e	a
cerastes	u	k	a	y	a	y	y	u	u	p	e	a	a	a	a
durissus	y	f	a	y	a	y	y	a	a	a	a	a	a	a	a
enyo	y	p	a	y	a	y	y	y	y	y	k	k	e	e	a
horridus	y	a	?	y	a	y	u	a	a	a	a	a	a	a	a
intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
lepidus	p	y	a	y	a	y	y	y	y	y	y	y	u	j	j
miliarius	g	u	c	y	a	y	y	y	y	y	y	p	a	a	a
mitchellii	u	e	a	y	a	y	u	m	i	e	e	e	a	a	a
molossus	y	u	a	y	a	y	y	e	a	a	a	a	a	a	a
polystictus	q	u	a	y	a	y	y	y	y	y	y	i	i	a	a
pricei	k	y	b	y	a	y	y	y	y	y	y	y	u	p	p
pusillus	y	a	?	y	a	y	y	y	y	y	y	a	a	a	a
ravus	?	m	c	y	a	y	y	y	y	y	y	m	m	m	m
ruber	y	k	a	y	a	y	p	e	a	a	a	a	a	a	a
scutulatus	y	k	a	y	a	y	y	u	u	j	e	a	a	a	a
stejnegeri	?	a	?	y	a	y	y	y	y	y	y	a	a	a	a
tigris	y	u	{a,c}	y	a	y	y	y	y	k	k	a	a	a	a
tortugensis	?	a	?	?	a	y	y	y	m	a	a	a	a	a	a
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	y	m	a	y	a	y	y	y	y	y	y	u	p	p	a
unicolor	y	q	{a,c}	y	a	y	y	s	m	g	a	a	a	a	a
vegrandis	y	a	?	y	a	y	y	y	m	a	a	a	a	a	a
viridis	y	k	a	y	a	y	y	y	y	k	a	a	a	a	a
willardi	y	g	a	q	a	y	y	y	y	y	m	a	a	a	a
bilineatus	y	m	c	y	y	y	y	y	m	a	a	a	a	a	a
contortrix	k	y	c	a	k	y	y	y	a	a	a	a	a	a	a
piscivorus	y	a	?	a	y	y	p	e	a	a	a	a	a	a	a
muta	a	u	a	y	y	m	i	e	a	a	a	a	a	a	a
blomhoffii	m	a	?	a	a	y	y	s	s	m	a	a	a	a	a

					200										210
adamanteus	a	a	a	y	y	p	y	y	y	e	a	u	e	u	a
aquilus	m	g	a	y	y	a	y	s	a	a	a	y	a	a	?
atrox	a	a	a	y	y	f	y	y	u	a	a	y	y	u	a
basiliscus	a	a	a	y	y	a	y	y	y	a	a	y	y	y	a
catalinensi	a	a	a	y	y	m	y	y	a	a	a	y	y	y	a
catenatus	a	a	a	y	y	p	y	p	a	a	a	y	a	p	y
cerastes	a	a	a	y	y	f	p	e	a	a	a	y	u	k	a
durissus	a	a	a	y	y	a	y	y	p	j	a	y	p	g	a
enyo	a	a	a	y	y	a	y	k	a	a	a	y	y	y	a
horridus	a	a	a	y	y	f	y	y	k	a	a	y	p	u	a
intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
lepidus	e	a	a	y	y	k	y	e	a	a	a	y	k	s	i
miliarius	a	a	a	y	y	p	y	p	a	a	a	y	a	y	a
mitchellii	a	a	a	y	y	i	y	q	i	a	a	y	u	i	a
molossus	a	a	a	y	y	a	y	y	p	a	f	y	p	y	a
polystictus	a	a	a	y	y	e	y	y	m	a	q	y	y	a	?
pricei	p	j	e	y	y	a	y	p	a	a	a	p	a	s	q
pusillus	a	a	a	y	y	a	y	y	y	a	a	y	a	y	y
ravus	a	a	a	y	y	a	y	m	a	a	a	y	a	a	?
ruber	a	a	a	y	y	p	y	y	y	a	f	y	k	p	a
scutulatus	a	a	a	y	y	f	y	u	e	a	a	y	e	y	a
stejnegeri	a	a	a	y	y	a	y	y	y	a	a	y	y	?	?
tigris	a	a	a	y	y	y	y	u	a	a	a	u	a	g	a
tortugensis	a	a	a	y	y	a	y	y	y	a	a	y	a	?	?
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	a	a	a	y	y	a	y	p	a	a	a	y	a	a	?
unicolor	a	a	a	y	y	a	y	y	y	s	q	y	q	i	a
vegrandis	a	a	a	y	y	a	y	y	m	a	a	y	y	?	?
viridis	a	a	a	y	y	f	y	k	a	a	a	y	p	k	a
willardi	a	a	a	y	y	m	y	y	g	a	a	y	y	a	?
bilineatus	a	a	a	y	y	y	y	y	y	a	a	m	m	y	y
contortrix	a	a	a	y	y	u	y	y	k	a	a	y	y	y	y
piscivorus	a	a	a	y	y	u	y	y	p	e	a	y	k	f	y
muta	a	a	a	e	e	i	y	y	y	u	y	y	y	y	y
blomhoffii	a	a	a	y	s	y	y	s	g	a	a	y	y	q	y

					215										225
adamanteus	a	k	a	p	y	y	a	e	a	a	y	y	a	y	a
aquilus	?	q	a	y	y	y	?	y	y	?	?	a	y	?	a
atrox	a	a	a	s	y	y	f	e	a	f	u	i	a	u	a
basiliscus	a	s	g	y	y	y	a	y	a	a	y	a	a	y	a
catalinensi	a	y	a	a	y	a	a	a	a	a	y	a	m	a	a
catenatus	i	e	a	p	y	y	a	y	u	y	y	f	s	u	a
cerastes	a	e	a	y	y	k	a	y	u	f	y	a	y	f	a
durissus	a	a	a	g	y	y	a	y	a	a	y	g	a	a	s
enyo	a	s	a	s	y	q	a	y	a	a	m	a	y	a	a
horridus	a	a	a	y	y	u	a	p	e	a	y	k	a	a	k
intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
lepidus	a	e	a	y	y	u	a	y	g	a	y	a	y	u	p
miliarius	a	a	a	g	y	q	a	y	s	g	y	a	y	f	a
mitchellii	a	m	a	u	y	y	a	s	a	a	d	a	i	m	a
molossus	a	e	a	y	y	y	a	u	j	a	y	a	a	k	a
polystictus	?	u	a	q	y	u	a	s	a	a	y	a	y	y	i
pricei	i	y	u	y	y	k	a	u	j	a	y	a	y	q	f
pusillus	a	a	a	y	y	y	?	a	a	?	?	a	y	?	y
ravus ?	m	a	y	y	y	?	y	y	?	?	a	y	y	a	
ruber	a	a	a	u	y	y	a	e	a	a	y	f	a	f	f
scutulatus	a	a	a	y	y	k	a	u	a	a	y	a	a	y	a
stejnegeri	?	y	a	y	y	y	?	?	?	?	y	a	y	y	a
tigris	a	e	e	y	y	y	a	a	a	a	a	a	p	i	a
tortugensis	?	?	?	y	y	y	?	?	?	?	?	a	a	y	a
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	?	i	a	q	y	y	?	y	y	?	?	a	y	?	i
unicolor	a	a	a	a	y	q	a	a	a	a	y	a	a	y	i
vegrandis	?	?	?	?	y	y	?	?	?	?	?	m	?	?	a
viridis	a	a	a	u	y	a	a	u	a	f	y	a	f	a	a
willardi	?	a	a	y	y	a	a	m	m	a	y	a	y	y	g
bilineatus	a	y	y	?	m	a	y	y	y	a	a	y	a	y	a
contortrix	u	u	e	y	f	a	y	y	p	a	a	a	u	a	a
piscivorus	a	p	j	y	a	a	y	y	u	a	a	a	f	f	f
muta	g	y	s	a	y	y	y	y	q	a	?	y	a	a	f
blomhoffii	a	y	y	?	y	i	a	y	m	?	y	a	y	i	a

					230										240
adamanteus	a	p	a	a	y	y	y	y	i	a	a	y	p	k	k
aquilus	y	a	?	?	a	a	a	m	y	a	a	y	s	a	a
atrox	a	p	a	q	y	y	u	y	e	a	a	y	p	a	a
basiliscus	a	y	a	s	y	y	y	y	m	a	a	y	y	a	a
catalinensi	a	a	?	?	y	y	a	y	y	a	a	y	y	a	a
catenatus	k	k	a	m	u	j	a	y	y	p	e	y	p	a	a
cerastes	a	y	a	f	y	a	a	u	y	y	a	y	y	p	e
durissus	a	y	a	y	y	y	y	y	g	a	a	y	k	a	a
enyo	u	y	a	a	y	u	a	y	y	p	a	y	u	a	a
horridus	p	y	a	f	y	y	p	y	y	a	a	y	u	k	a
intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
lepidus	y	a	?	?	a	a	a	p	y	p	a	y	y	e	a
miliarius	y	k	a	a	e	a	a	y	y	y	a	y	y	e	a
mitchellii	q	u	a	y	u	p	a	y	y	a	a	y	p	e	e
molossus	a	y	a	y	y	y	p	y	a	a	a	y	y	a	a
polystictus	u	m	b	?	y	y	a	y	a	a	a	y	y	a	a
pricei	y	f	a	a	a	a	a	a	y	y	a	y	y	a	a
pusillus	y	a	?	?	y	y	a	y	y	y	y	y	y	a	a
ravus	y	a	?	?	m	a	a	y	y	a	a	y	y	a	a
ruber	k	y	a	y	y	y	y	y	a	a	a	y	u	a	a
scutulatus	p	y	a	y	y	p	e	y	y	p	a	y	y	e	a
stejnegeri	y	a	?	?	a	a	a	y	y	y	a	y	a	a	a
tigris	y	a	?	?	y	u	a	a	y	s	a	y	y	y	u
tortugensis	a	y	a	y	y	y	y	y	a	a	a	y	a	a	a
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	y	a	?	?	k	a	a	y	y	u	a	y	y	a	a
unicolor	a	y	a	s	y	y	s	y	i	a	a	a	a	a	a
vegrandis	a	y	?	y	y	y	y	y	a	a	a	y	m	a	a
viridis	y	y	a	a	y	p	j	y	y	a	a	y	u	p	e
willardi	y	a	?	?	m	g	a	i	y	y	m	y	s	g	g
bilineatus	m	m	a	a	y	y	a	y	y	a	a	y	y	a	a
contortrix	y	f	a	a	y	y	a	y	y	a	a	y	u	a	a
piscivorus	y	k	a	a	u	u	a	y	y	a	a	y	y	k	a
muta	a	i	a	y	y	u	u	y	y	d	a	y	y	e	e
blomhoffii	y	g	b	?	g	g	a	y	q	a	a	y	s	a	a

					245										255
adamanteus	u	u	a	a	a	p	e	m	f	s	a	y	u	e	a
aquilus	y	q	?	?	s	y	y	?	?	?	?	?	?	?	?
atrox	u	u	a	a	a	y	u	a	u	y	a	k	a	a	a
basiliscus	g	a	m	a	a	y	s	y	y	m	a	y	m	a	a
catalinensi	y	a	a	a	m	y	m	y	a	y	a	y	a	a	a
catenatus	u	j	f	a	f	y	y	f	y	p	a	u	a	a	a
cerastes	k	a	a	a	a	y	y	u	y	y	a	y	p	a	a
durissus	k	a	a	a	a	y	y	y	a	y	a	y	y	a	a
enyo	u	u	a	a	a	y	y	m	y	m	m	y	a	a	a
horridus	y	y	a	f	a	y	u	f	u	y	a	y	k	a	a
intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
lepidus	p	p	f	a	a	y	y	y	s	y	m	y	s	g	a
miliarius	a	a	a	a	a	y	y	s	y	y	g	y	m	a	a
mitchellii	q	m	i	a	m	y	y	y	m	y	a	y	m	a	a
molossus	e	a	a	a	a	y	y	u	y	y	p	s	g	a	a
polystictus	m	i	y	a	a	y	q	a	a	?	?	y	a	a	a
pricei	y	y	i	a	s	y	p	y	y	y	a	y	i	a	a
pusillus	y	y	?	?	a	y	y	?	?	?	?	?	?	?	?
ravus	m	m	?	?	a	y	y	?	?	?	?	?	?	?	?
ruber	a	a	a	a	a	y	y	u	y	y	f	y	k	a	a
scutulatus	e	e	k	a	a	y	y	k	u	k	a	u	j	a	a
stejnegeri	?	?	?	?	y	y	y	?	?	?	?	?	?	?	?
tigris	y	p	a	a	a	y	y	m	m	y	a	y	m	m	a
tortugensis	y	y	?	?	a	y	y	?	?	?	?	?	?	?	?
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	p	p	?	?	k	y	y	?	?	?	?	?	?	?	?
unicolor	a	a	a	a	a	y	i	y	a	?	?	y	y	a	a
vegrandis	a	a	?	?	a	y	y	?	?	?	?	?	?	?	?
viridis	p	p	a	a	a	y	y	p	p	y	a	u	u	p	e
willardi	q	i	a	a	g	y	y	y	y	y	a	y	y	y	a
bilineatus	y	y	a	a	y	y	y	y	y	y	y	y	y	a	a
contortrix	k	k	y	a	y	y	y	m	s	y	s	y	g	a	a
piscivorus	k	k	k	a	u	y	u	f	y	u	a	y	p	e	a
muta	a	a	?	y	y	y	y	?	?	?	?	?	?	?	?
blomhoffii	g	a	a	a	y	y	y	y	y	a	y	y	y	a	y

					260										270
adamanteus	k	e	a	a	u	e	y	a	y	f	k	y	p	y	y
aquilus	y	a	a	a	y	y	y	g	s	a	?	m	g	y	s
atrox	y	u	j	a	y	e	y	a	y	a	f	y	y	y	y
basiliscus	y	s	g	a	y	m	y	g	y	g	y	y	s	y	y
catalinensi	y	y	a	a	y	y	y	a	y	a	y	m	m	m	a
catenatus	y	k	a	a	y	y	a	a	y	f	u	u	j	u	p
cerastes	y	p	e	a	y	p	y	a	y	p	u	p	a	p	j
durissus	y	m	m	a	y	q	y	k	y	a	a	y	y	y	y
enyo	y	a	a	a	y	y	y	a	y	a	m	y	k	y	k
horridus	y	y	k	a	p	a	y	a	y	a	p	y	u	y	y
intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
lepidus	y	u	e	e	y	g	y	f	u	f	s	u	e	u	j
miliarius	y	y	a	a	y	m	k	a	y	a	y	y	e	u	p
mitchellii	y	a	a	a	m	a	y	a	y	g	q	u	u	u	p
molossus	y	g	a	a	y	m	y	a	y	a	a	y	y	y	y
polystictus	y	m	a	a	q	a	y	f	u	p	a	y	u	y	y
pricei	y	q	a	a	y	q	k	k	u	f	i	p	a	u	p
pusillus	y	y	y	a	?	?	y	a	y	?	?	y	a	y	y
ravus	?	?	?	?	?	?	y	a	y	m	?	m	a	y	m
ruber	y	y	p	a	p	j	u	f	y	a	k	y	u	y	p
scutulatus	y	k	a	a	u	p	y	f	y	p	f	y	e	p	j
stejnegeri	?	?	?	?	?	?	y	a	y	a	?	?	?	?	?
tigris	s	a	a	a	y	g	y	a	y	y	y	y	a	p	a
tortugensis	y	m	a	a	?	?	y	a	y	a	?	q	q	m	m
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	?	?	?	?	?	?	y	a	y	a	?	y	k	y	p
unicolor	y	a	a	a	y	a	y	a	y	i	y	y	y	y	y
vegrandis	?	?	?	?	?	?	y	a	y	y	?	y	y	y	y
viridis	y	p	e	a	y	u	y	a	y	f	f	y	e	y	k
willardi	y	a	a	a	y	y	s	a	y	a	y	s	m	s	m
bilineatus	y	m	a	a	y	a	y	a	y	y	a	y	m	y	y
contortrix	y	p	a	a	y	k	y	a	y	f	m	y	g	y	y
piscivorus	u	j	a	a	y	p	y	a	y	f	u	y	k	y	u
muta	y	u	a	a	s	a	y	u	e	a	?	y	u	y	y
blomhoffii	a	y	a	y	i	y	y	s	y	y	s	a	y	a	a

					275										285
adamanteus	y	g	y	y	y	g	p	p	y	y	y	u	y	y	p
aquilus	y	?	?	?	?	?	?	g	?	y	q	y	y	m	I
atrox	y	a	y	y	s	g	u	a	y	y	k	y	e	e	k
basiliscus	y	y	y	y	y	a	m	a	y	y	s	m	y	m	m
catalinensi	y	a	y	y	y	a	y	y	y	y	a	y	y	y	y
catenatus	u	a	u	p	a	a	u	f	a	y	a	u	p	e	k
cerastes	u	a	u	a	a	a	u	p	u	y	a	y	u	p	a
durissus	y	y	y	y	y	a	y	a	a	y	f	u	u	e	k
enyo	y	a	y	y	a	a	m	a	y	y	a	y	y	m	g
horridus	y	a	y	u	a	a	y	a	s	y	m	y	y	m	a
intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
lepidus	y	a	y	g	a	a	y	u	u	y	u	y	p	e	f
miliarius	y	a	y	a	a	a	a	k	g	y	f	y	k	k	f
mitchellii	s	a	m	m	a	a	y	a	q	u	k	y	y	q	q
molossus	y	a	y	y	p	a	p	a	p	y	f	u	y	u	y
polystictus	y	a	y	y	y	a	y	a	q	u	y	y	y	p	a
pricei	y	a	q	i	a	a	y	k	y	y	k	y	y	y	q
pusillus	y	?	?	?	?	?	?	a	y	y	a	y	a	a	y
ravus	y	?	?	?	?	?	?	a	?	y	m	y	y	y	a
ruber	y	f	y	y	a	a	f	u	y	y	f	u	u	p	f
scutulatus	y	f	y	y	u	a	u	m	y	y	y	y	u	p	f
stejnegeri	y	?	?	?	?	?	?	a	y	y	y	y	a	a	a
tigris	y	a	y	i	a	a	y	f	y	y	k	a	y	e	u
tortugensis	y	?	?	?	?	?	?	a	y	y	y	y	a	a	a
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	y	?	?	?	?	?	?	p	y	y	m	y	y	y	m
unicolor	y	?	?	?	?	?	?	a	y	y	i	i	q	i	m
vegrandis	y	?	?	?	?	?	y	a	?	y	y	y	a	a	a
viridis	u	a	u	u	j	a	y	f	y	y	a	y	y	p	f
willardi	y	a	y	a	a	a	a	a	m	s	a	y	y	s	y
bilineatus	y	a	y	y	a	a	y	m	y	y	y	y	m	m	m
contortrix	m	a	y	g	a	a	k	u	a	y	y	y	y	y	a
piscivorus	y	a	u	a	a	a	y	a	u	y	a	y	k	a	y
muta	u	?	?	?	?	?	?	a	y	u	u	y	s	m	a
blomhoffii	a	y	m	q	y	m	y	y	y	y	a	s	m	a	a

					290										300
adamanteus	p	y	y	y	y	a	y	p	k	a	m	y	a	s	a
aquilus	?	m	g	s	a	a	m	s	s	m	?	?	?	?	?
atrox	a	y	y	y	y	a	y	f	p	a	a	y	a	u	a
basiliscus	a	y	y	y	y	y	y	y	i	g	m	y	a	?	?
catalinensi	a	m	a	y	a	a	y	m	m	a	y	y	a	y	a
catenatus	a	u	a	p	k	a	u	f	a	a	f	y	a	u	e
cerastes	a	e	e	k	k	a	k	f	k	a	k	y	a	u	a
durissus	a	y	y	y	y	p	y	u	f	a	y	y	a	y	a
enyo	a	y	p	y	p	a	y	f	a	a	y	a	a	m	a
horridus	a	y	y	y	y	e	y	a	u	a	u	y	a	s	a
intermedius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
lepidus	a	u	e	y	e	a	u	f	p	a	i	y	a	q	a
miliarius	a	u	e	k	a	a	f	a	a	f	m	y	a	y	g
mitchellii	a	u	u	u	y	e	m	e	a	a	g	y	a	y	a
molossus	a	y	y	y	y	y	y	u	f	a	a	y	a	y	a
polystictus	a	y	y	y	y	i	y	u	a	a	a	a	a	y	a
pricei	a	k	a	k	a	a	f	a	p	a	i	y	a	q	a
pusillus	?	y	y	y	y	a	y	y	y	a	?	?	a	?	?
ravus	?	y	m	y	m	a	y	y	m	m	?	?	a	?	?
ruber	a	y	y	y	p	a	y	k	k	a	k	y	a	y	a
scutulatus	g	y	y	y	k	e	y	m	u	a	g	y	a	y	a
stejnegeri	a	y	y	y	a	a	y	y	a	a	?	?	a	?	?
tigris	a	y	a	u	u	a	p	k	f	a	i	y	a	y	a
tortugensis	?	y	y	y	m	a	y	a	a	y	?	?	a	?	?
transversus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
triseriatus	?	y	k	p	a	a	f	a	f	a	?	?	a	?	?
unicolor	a	y	y	y	y	y	y	i	a	a	y	y	a	y	a
vegrandis	?	y	y	y	y	a	y	m	a	a	?	?	a	?	?
viridis	a	p	a	y	p	a	y	y	p	a	u	y	a	y	a
willardi	?	y	m	y	g	a	y	m	a	a	y	y	a	y	a
bilineatus	a	y	y	y	a	a	y	m	a	a	a	y	y	y	a
contortrix	a	u	a	k	a	a	k	k	a	k	p	y	a	y	a
piscivorus	a	y	u	y	p	e	k	y	f	y	a	y	a	y	e
muta	?	y	y	y	y	y	e	u	a	y	?	?	a	?	?
blomhoffii	a	a	a	g	a	y	y	a	y	a	a	y	a	a	a

					305					310	
adamanteus	a	y	y	a	a	y	y	a	y	b	b
aquilus	?	?	?	?	a	y	y	a	a	b	b
atrox	a	y	y	a	a	u	p	a	p	b	b
basiliscus	m	?	y	m	a	y	s	a	y	b	b
catalinensi	a	y	y	y	a	y	a	a	a	b	b
catenatus	f	y	y	a	a	y	y	y	k	b	a
cerastes	a	y	y	a	k	y	y	i	a	b	b
durissus	a	y	a	a	a	q	q	a	k	b	b
enyo	a	y	y	a	a	y	i	a	a	b	b
horridus	a	u	y	a	a	u	u	a	p	b	b
intermedius	?	?	?	?	?	?	?	?	?	b	b
lepidus	a	y	y	a	a	y	q	a	a	b	b
miliarius	a	y	y	g	a	y	y	y	a	b	a
mitchellii	a	y	y	g	a	u	q	a	p	b	b
molossus	a	y	y	g	a	u	e	a	u	b	b
polystictus	a	y	y	a	a	p	p	a	s	b	b
pricei	a	y	y	a	a	y	y	g	a	b	b
pusillus	?	?	?	?	a	y	a	a	y	b	b
ravus	?	?	?	?	a	y	y	a	m	b	a
ruber	f	y	y	e	a	u	p	a	k	b	b
scutulatus	a	y	y	e	a	u	a	a	u	b	b
stejnegeri	?	?	?	?	a	y	y	a	a	b	b
tigris	y	y	y	a	a	y	u	a	a	b	b
tortugensis	?	?	?	?	a	a	a	a	y	b	b
transversus	?	?	?	?	?	?	?	?	?	b	b
triseriatus	?	?	?	?	a	y	y	a	m	b	b
unicolor	a	?	y	a	a	a	a	a	y	b	b
vegrandis	?	y	?	?	?	?	?	?	y	b	b
viridis	a	y	y	a	a	y	p	a	u	b	b
willardi	a	y	y	a	a	q	q	a	g	b	b
bilineatus	a	y	y	y	a	y	y	a	a	a	a
contortrix	a	y	u	u	f	y	y	a	p	a	a
piscivorus	a	p	y	q	a	k	a	a	a	a	a
muta	?	?	?	?	a	y	y	g	e	a	b
blomhoffii	y	y	a	a	a	a	y	a	y	y	a

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NDS data set
            1        10        20        30        40        50        60        70        80
adamanteus  CACCACAAC3C332232CAAA3CCAA232A3A2AACA3222CC3AA3CAC2CCAACCA3CA3C33AACAA3C33C33C3C
aquilus     CACCACAAC3C332232CAAA3CCAA232A3A2AACA3222CC3AAC3ACACCAACCA33A3CC3AACAA3C33CC3C3C
atrox       CACCACAAC3C332232CAAA3CCAA232A3A2AACA3222CC3AA3CAC2CCAACCA3CA3C33AACAA3C33C33C3C
basiliscus  2ACCACA333C332232CAA23CCAA232A3A2AA3A3222CC3AACCACACC3ACCA3CA3C33AACAA3333C33C32
bilineatus  ????????????????????????????????????????????????????????????????????????????????
blomhoffii  ????????????????????????????????????????????????????????????????????????????????
catalinensis????????????????????????????????????????????????????????????????????????????????
catenatus   --------------------33CCAA232A3A2AA3A3222CC3AACCACACCAACCA3CA3CA3AACAA3C33C33A3C
cerastes    ????????????????????????????????????????????????????????????????????????????????
contortrix  C2CCAAAAC3C332232CAAA3CCAA23AA3A2AA3A32A2CC3AACCACACCAAC3A3CA33C32ACAA3C33CC3C3C
durissus    CACCACAAC3C332232CAA23CCAA232A3A2AA3A322ACC3AACCACACCAACCA33ACCC3AACAA3C33C33C3C
enyo        ????????????????????????????????????????????????????????????????????????????????
horridus    32CCACAAC3C332232CAA23C3AA232A3A2AA3A3222CC3AAC3A3ACCAACCA3CA3CC32ACAA3C33C33C3C
intermedius ????????????????????????????????????????????????????????????????????????????????
lepidus     C2CCACAAC3C332232CAAA3CCAA232A3A2AA?A3222CC3AAC3ACACCAACCA33A3C33AACAA3C33C33A3C
miliarius   -ACCACAA33C332232CAA23CAA3232A3A2AACA322ACC23ACCACACC2AC3A33A3A33AACAA3333CC3C3C
mitchelli   ????????????????????????????????????????????????????????????????????????????????
molossus    CACCACAAC3C332232CAA23CCAA232A3A2AA3A3222CC3A2CCACACCAACCA3CA3CC3AACAA3C33C33C3C
muta        ????????????????????????????????????????????????????????????????????????????????
piscivorus  C2CCAAAAC3C332232CAAA3CCAA23223A2AA3A3222CC3AACAACACCAAC3A3CA3CC32ACA23C33CC3C3C
polystictus C2CCACAAC3C332232CAA23CCAA232A3A2AACA3222CC3AA3CAC2CCAACCA3CA3C33AAC2A3C33C33C3C
pricei      CACCACA3C3C332232CAAA3CCAA232A3A2AACA322ACC3AA33ACACCAACAA3CACCC3AACAA3C33C33C3C
pusillus    ----------------------CCAA232A3A2AA3A322ACC3AA33ACACCAACCA3CA3C??AACAA3C33C33C3C
ravus       CACCACAAC3C332232CAAA3CCAA232A3A2AACA3222CC3AA3CACACCAACCA3CA3C33AAC2A3333C33C3C
ruber       CACCACAA33C332232CAA23CCAA232A3A2AA3A322ACC3AA33ACACCAACCA3CA3C33AACAA3C33C33C3C
scutulatus  --------------------------------------------------------------------------------
stejnegeri  --------------------------------------------------------------------------------
tigris      --------------------A3CCAA232A3A2AA3A322ACC3AA3CAC2CCAACCA3CACC33AAC2A3C33C33A3C
tortugensis CACCACAAC3C332232CAAA3CCAA232A3A2AACA3222CC3AA3CACACCAACCA3CA3C33AACAA3C33C33C3C
transversus CACCACA3C3C332232CAAA3CCAA232A3A2AACA3222CC3A233ACACCAACCA33A3CC3AACAA3333C33C3C
triseriatus CACCACAAC3C332232CAAA3CCAA232A3A2AACA3222CC3AAC3ACACCAACCA33A3CC3AACAA3C33CC3C3C
unicolor    CACCACAAC3C332232CAA23CCAA232A3A2A23A3222CC3AACCACACCAACCA3CACCC3AACAA3C33C33C3C
vegrandis   CACCACAAC3C332232CAA23CCAA232A3A2AA3A322ACC3AACCACACCAACCA33ACCC3AACAA3C33C33C3C
viridis     --------------------------------------------------------------------------------
willardi    CACCACA3C3C332232CAAA3CCAA232A3A2AACA322ACC3AA33ACACCAACAA3CACCC3AACAA3C33C33C3C
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             81        90        100       110       120       130       140       150       160
adamanteus   CCTACTCACCTCCACAATTTGACCCTCCCATAAAAATAGTCTCAACAACACTAAACACACATTAATATTAATATTCATAA
aquilus      CCTGGTCGCCTCCACAATTCGACCCACCCCTAAAC???????????ATCC?AAATACGTCCTCATACTAATATTCATAA
atrox        CCTACTCACCTCCACAATTTGACCCTCCCATAAAAATAGTCACAACAACACTAAACACACATTAATATTAATATTCATAA
basiliscus   CCTAATCGCCTCCACAATTCGACCCTACCATAAAAATAGCCTCAACGACACTAAACACACTCTAATGCTAATATTCATAA
bilineatus   ????????????????????????????????????????????????????????????????????????????????
blomhoffii   ????????????????????????????????????????????????????????????????????????????????
catalinensis????????????????????????????????????????????????????????????????????????????????
catenatus    TCTAACCGCCTCCACAATCTGACCCACCCAAAAACACAACCTCAATAACATTAAGTACACCCTTATACTAATATCTATAA
cerastes     ????????????????????????????????????????????????????????????????????????????????
contortrix   CCTGACTGCCTCTACAATCCGCCCTCTCCCCAAACACAACCTCAGCAACACTAAACACACCCTAATATTAATATTCATAA
durissus     ACTAATCGCCTCCACAATTTGACCCTCCAATAAAAAAGACCACAACAACACTAAATACAACCTGATATTAATATTCATAA
enyo         ????????????????????????????????????????????????????????????????????????????????
horridus     CCTAGCTGCCTCCACAATTCGACCCCTCCCTAAACACAGCCTCAATGATACTAAATACACCTTAATACTAATGTTCATAA
intermedius  ????????????????????????????????????????????????????????????????????????????????
lepidus      CCTAATCGCCTCCACAATTCGACCCACCCCTAAACACAGCC?CAACGACACTAAATACATCCT?ATACTAATATTCATAA
miliarius    TTTAACCGCCTCTACAATCCGACCTACCCATAAGCACAACCTTAATAACACCAAATATACCATAATACTAATATTTATAA
mitchelli    ????????????????????????????????????????????????????????????????????????????????
molossus     CCTAGTTACCTCCACAATTTGACCCTCCTACAAAAATAGCCTCAACAACACTAAACACACTTTAATACTAATATTCCTAA
muta         ????????????????????????????????????????????????????????????????????????????????
piscivorus   ACTAACCGCTTCTACAATTCGCCCCACCCCTAAACATAAGCTCAACAACACTAAATACACCCTAATACTAATATTCATAA
polystictus  CCTAATTATCTCCGCAGTACTACCCACCCCCAAACACGGCCTCAACAACACCAACTACACCTTGATACTAATATTCATAA
pricei       CCTAGCCGCCTCCACAGTTTTATTCACCCAAAAACAAACCCTCAATGAAATCAAATACATGTTAATACTAATATTCATGA
pusillus     CCTAGTCGCCTCCACAATTTGA????????????????????????????????????????????????????????
ravus        CCTAGTCTCCTCCACAATCCGACCCACCCTTAAACACGACCTCAACGGCACCAAACACACCCTAATACTAATATTTGTAA
ruber        CCTATTCACCTCCACAATTTGACCCGCCCCCAAAAA?AGCCCCAACAACACTAAACACACCCTAATACTAATGTTCATAA
scutulatus   --------------------------------------------------------------------------------
stejnegeri   --------------------------------------------------------------------------------
tigris       CCTAATCACCTCCACAATTCGACCTTCTCCTAAAAATGACCTCAACAACACCAAATATACCCTAATACTAATATTCATAA
tortugensis  CCTACTCACCTCCACAATTTGACCCACCCATAAAAATAGCCTCAACAACACTAAACACACATTAATATTAATATTCATAA
transversus  CCTAACCGCCTCCACAATCCTACCCACCCAAAACCGAACCCTTAATGACACCAAATATACCCTAATACTGATATTTATAA
triseriatus  CCTGGTCGCCTCCACAATTCGACCCACCCCTAAAC???????????ATCTCAAATACGTTCTCATACTAATATTCATAA
unicolor     ACTAATCGCTTCCACAATTCGACCCTCCAGTAAAAAGACCCGCAACAACACTAAGTACAACCTGATATTGATATTCATAA
vegrandis    ACTAATCGCCTCCACAATTTGACCCTCCAATAAAAAAGACCACAACAACACTAAATACAACCTGATATTAATATTCATAA
viridis      --------------------------------------------------------------------------------
willardi     CCTAGCCGCCTCCACAGTTTTATTCACCCAAAAACAAACCCTCAATGAAATCAAATACATCTTAATACTAATATTCATGA
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             161     170       180       190       200       210       220       270       240
adamanteus   TTAGCATGATCCCCCTGAACACCATACTAAACAACAATAATGAGCTAACAATAACACTATACCCCCTAGTCACGACCCAA
aquilus      TTAGCCTGATCCCTCTCAACACCACACTAAACAACAACAATGA??????????CACTATC{AT}CCCCTAGTTCTAACC
atrox        TTAGCATGATCCCCCTGAACACCATACTAAACAACAATAATGAGCTAACAATAACACTATACCCCCTAGTCACGACCCAA
basiliscus   TTAGCATAATCCCACTAAACACCATACTAAACAACAATAATGAACTAACAATAACACTACACCCCCTGATCACAACCCAA
bilineatus   ????????????????????????????????????????????????????????????????????????????????
blomhoffii   ????????????????????????????????????????????????????????????????????????????????
catalinensis????????????????????????????????????????????????????????????????????????????????
catenatus    TTAGCCTAATCCCCCTCAACACTATATTACACTATAACAACGAACTATCAATAACATTATTACCTCTAATCATTACTCAA
cerastes     ????????????????????????????????????????????????????????????????????????????????
contortrix   TCAGCACTATCCCCCTCAATACCCTACTAAACAACAACGACGAACTAACAATAACACTATTCCCCTTAATCATAACCCCA
durissus     TTAGCATAATTCCACTAAACAGCACACTAAACAACAACAACGAACTAACATTAACACTACACCCCATAATCATAACACAG
enyo         ????????????????????????????????????????????????????????????????????????????????
horridus     TTAGTATGATCCCTCTCAACCCCCTATTAAACAATAACAGCGAACTAACAATAACACTATTGCCCCTAATTACAACCCAG
intermedius  ????????????????????????????????????????????????????????????????????????????????
lepidus      TTAGCACAATCCCTCTCAACACCACACTAAACAACAATAATGGGCTAACAATAACGCTACGCCCCCTAATCCTAACCCAA
miliarius    TTAGCCTAATTCCACTAAACACCATATGACACAACAACAACGAACTATCAATAACACTTATACCTTTAGTTATAACCCAA
mitchelli    ????????????????????????????????????????????????????????????????????????????????
molossus     TTAGCATGATCCCTCTAAACACTATACTAAACAACAATAATGAGCTAACAATAACACTACACCCCCTGATCATAACCCAG
muta         ????????????????????????????????????????????????????????????????????????????????
piscivorus   TTAGCCTAATCCCCCTTAACACACTATTAAACAATAACAACGAACTAACAATAACGCTATTCCCCCTAATTACAACTCCA
polystictus  TTAGCACGATCCCGCTCAACACCATACTAAACAACAATACTGAGCTAACAATAACACTGTTTTCCCTAATCACCACCCAA
pricei       TTAGCATGATTCCTCTCAACATAACACTAAACAACAATAATGAACTAACAATAACATTAACACCTCTAATTATTACCCAA
pusillus     ????????????????????????????????????????????????????????????????????????????????
ravus        TCAGCTTGATCCCCCTCAACATTATACTAAATAACAATAATGAACTAACAATAACACTATCCCCCCTAATTATAACCCAA
ruber        TTAGCATGATCCCCCTGAACACCATACTAAACAACAACAATGAACTAACAATAACACTATCCCCCTGGATCATAACCCA?
scutulatus   --------------------------------------------------------------------------------
stejnegeri   --------------------------------------------------------------------------------
tigris       TTAGCATAATCCCCCTGAACAATACACTAAATAATAACAACGAACTAACAATTACACTATGCCCCCTAATAATAACCCAA
tortugensis  TTAGCATAATCCCCCTGAACACCATACTAAACAACAATAATGAGCTAACAATAACACTATACCCCTGGTTCACAACCCAG
transversus  TTAGCATAATTCCTCTTAACACCATTATAAATAACAATAACGAACTAACAATAACACTACTACCCCTAATCTTTACCCAA
triseriatus  TTAGCCTGATCCCTCTCAACACCGCACTAAACAACAACAATGAGCTAACAATAACACTATCCCCCCTAGTTCTAACCCAG
unicolor     TTAGCATAATCCCACTAAACAGCACACTAAACAACAACAGCGAACTAACATTAACACTATATCCCATAATCACGACACAG
vegrandis    TTAGCATAATTCCACTAAACAGCACACTAAACAACAACAACGAACTAACATTAACACTACACCCCATAATCATAACACAG
viridis      --------------------------------------------------------------------------------
willardi     TTAGCATGATTCCTCTCAACATAACACTAAACAACAATAATGAACTAACAATAACATTAACACCTCTAATTATTACCCAA
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             241      250        260        270        280        290        300        310        320
adamanteus   0102020030313030330110330121332010101303113320133310331102302103323310330113202 1
aquilus      CAGACAGAAAACATCTACATTACCATCACACTTGACACGCTATCCTTAATCTTCATCCCAGTAGCACTATTCGTCACATG
atrox        ACAGAGAATATCTATATTACCATTACGCTTGACACACTATCCTTGACTTTCATTCCATGAGCATTGTTCATTACCTGAGC
basiliscus   ACAGAAAACATCTATATTTCCCTCACACTTGATACACTATCATTAATCTTCATCCCAATAGCATTGTTCGTCACCTGGTC
bilineatus   ??????????????????????????????????????????????????????????????????????????????
blomhoffii   ??????????????????????????????????????????????????????????????????????????????
catalinensis??????????????????????????????????????????????????????????????????????????????
catenatus    ACAGAGAATATCTATATTACCATTACACTTGACACCTTATCCTTAACCTTTATCCCAGTAGCACTATTTATCACATGGTC
cerastes     ??????????????????????????????????????????????????????????????????????????????
contortrix   ACAGAAAACATTAACATTTCTTTTACACTTGACACACTATCCTTAACCTTCATCCCAGTAGCATTATTCATCACGTGATC
durissus     ACAGAAAACATCTATATTTCCATTACACTTGACACACTATCATTAACCTTTATTCCAGTAGCATTATTCGTCACCTGGTC
enyo         ??????????????????????????????????????????????????????????????????????????????
horridus     ACAGAAAACATCTATATCACCATTACACTTGACACACTATCCTTAACCTTTATCCCAGTAGCACTGTTCATTACATGATC
intermedius  ??????????????????????????????????????????????????????????????????????????????
lepidus      ACAGAAAACATCTACATTACCATCACACTTGACACGTTATCCCTGATCTTCATCCCAGTAGCACTATTTGTCACATGATC
miliarius    ACAGAAAACATCTATATTTCCCTTACATTTGACACGCTATCCCTAACCTTCACCCCAGTAGCACTATTTATTACATGATC
mitchelli    ??????????????????????????????????????????????????????????????????????????????
molossus     ACAGAAAACATCTATATTTCCATCACACTTGACACACTATCACTAATCTTCATCCCAATAGCATTATTCGTCACCTGGTC
muta         ??????????????????????????????????????????????????????????????????????????????
piscivorus   ACAGAAAACAT?TATATCTCCCTCACACTCGATACACTATCCTTAACCTTTATCCCAGTAGCGCTATTCATTACATGATC
polystictus  ACGGAAAACATCTACATTACCCTTGCACTCGACACACTATCCTTAACCTTCATCCCAGCAGCACTATTCATTACATGATC
pricei       ACAGAAAACATCTATATTACTCTCACACTTGACATATTATCTCTAACCTTCATCCCAGTAGCACTATTTGTCACATGAGC
pusillus     ????????????????????????????????????TATC?CTGACTTT?ATTCCAGTAGCATTATT??T?ACATGA?C
ravus        ACAGAAAACATCTATATCACTATTACACTTGATACACTATCCCTAACCTTCATCCCAGTAGCATTATTTATTACATGATC
ruber        ACAGAGAACATCTATATTACCATTAC?CTTGACACACTATCCCTGACTTTTATTCCAGTAGCATTATTCATTACATGAAC
scutulatus   --------------------------------------------------------------------------------
stejnegeri   --------------------------------------------------------------------------------
tigris       ACAGAAAACATCTATGTTACCATTACACTTGACACACTATCCCTAACCTTCATCCCAGTAGCCTTATTTATTACCTGAGC
tortugensis  ACAGAGAATATCTATATTATAATTACGCTTGACACACTATCCTTGACTTTCATTCCAGTAGCATTATTCATTACCTGAGC
transversus  ACAGAAAACATCTATATCACCATTACACTTGACACATTATCTCTAATCTTCATCCCAGTAGCACTATTTATTACATGAGC
triseriatus  ACAGAAAACATCTACATTACCATCACACTTGACACGCTATCCTTAATCTTCATCCCAGTAGCACTATTCATCACATGGTC
unicolor     ACAGAAAACATCTATATTTCCATTACACTTGACACACTATCATTAACCTTTATTCCAGTAGCATTATTCGTCACCTGGTC
vegrandis    ACAGAAAACATCTATATTTCCATTACACTTGACACACTATCATTAACCTTTATTCCAGTAGCATTATTCGTCACCTGGTC
viridis      --------------------------------------------------------------------------------
willardi     ACAGAAAACATCTATATTACTCTCACACTTGACATATTATCTCTAACCTTCATCCCAGTAGCACTATTTCTCACATGAGC
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             321      330        340        350        360        370        380        390        400
adamanteus   CATCACTGAATTTTCCATGTGGTATATATCCTCAGACCCCTATATTAACAAATTCATTAAATACTTAACAACCTTCCTAA
aquilus      GTCTATTACTGAGTTCTCCATCTGATACATGTCCTCAGACCCAAATATCAACAAATTTATTAA?TATCTAATAGCCTTTC
atrox        CATCACTGAATTTTCCATGTGGTATATATCCTCAGACCCCTATATTAACAAATTCATTAAATACTTAACAACCTTCCTAA
basiliscus   TATTACTGAATTTTCCATTTGATACATGTCCTCAGACCCAAATATTAACAAGTTCATTAAATACCTAATAGCCTTTTTAA
bilineatus   ????????????????????????????????????????????????????????????????????????????????
blomhoffii   ????????????????????????????????????????????????????????????????????????????????
catalinensis????????????????????????????????????????????????????????????????????????????????
catenatus    TATCGTTGAATTCTCCATCTGATACATATCATCAGACCCTAATATCAACAAATTTATTAAGTATTTAACAACCTTTCTAA
cerastes     ????????????????????????????????????????????????????????????????????????????????
contortrix   CATTACTGAGTTCTCTACATGATACATGTCCTCCGACCCCAACATTAACAAATTCATTAAATACTTAATTACCTTCTTAA
durissus     CATTGTTGAATTTTCCATCTGGTACATATCCTCAGACCCAAATATTAACAAGTTCATTAATTACCTAATAACCTTTTTAA
enyo         ????????????????????????????????????????????????????????????????????????????????
horridus     CATCGTCGAGTTCTCCATCTGGTACATATCCTCAGACCCCAATATCAACAAGTTCATTAAATACCTAATCACCTTTCTAA
intermedius  ????????????????????????????????????????????????????????????????????????????????
lepidus      CATCACTGAGTTCTCCATCTGGTATATGTCATCAGACCCCAATATTAACAAATTTATTAAGTATCTAACGGCCTTTCTAA
miliarius    TATTATTGAATTTTCTATCTGATACATGTCCTCAGACCCCAATATTAACAAATTCATTAAATATTTAACAACCTTCTTAA
mitchelli    ????????????????????????????????????????????????????????????????????????????????
molossus     TATTACTGAGTTTTCCATGTGATACATGGCCTCAGATCCAAATATTAACAAGTTCATTAAATACTTAATAGCCTTTTTAA
muta         ????????????????????????????????????????????????????????????????????????????????
piscivorus   CATTACTGAATTCTCCATGTGATATATATCCTCTGACCCAAACATTAACAAATTCATTAAATACTTATCAGCCTTTTTAA
polystictus  CATCACTGAGTTCTCTATCTGGTACATATCCTCAGACCCCAATATTAACAAATTTATTAAATACCTAACAACCTTTCTAA
pricei       CATTGTCGAATTCTCCATTTGATACATAGCCTCAGACCCAAATATCAACAAATTCATTAAATATCTAATAACCTTTCTAA
pusillus     CAT???TGAATTTTCCATGTGGTATATA?CCTCAGATCCTAA?AT?AACAAATTCATTAAATA?TTAA?AGCCTT?CT?A
ravus        TATTACTGAGTTTTCCATCTGATATATGTCCTCAGACCCCAACATTAACAAATTTATTAAATACTTGATAACCTTTCTAA
ruber        CATCACTGAATTTTCCATGTGGTATATAGCCTCAGATCCTAACATTAACAAATTCATTAAATACTTAACAGCCTTCCTCA
scutulatus   --------------------------------------------------------------------------------
stejnegeri   --------------------------------------------------------------------------------
tigris       CATTACTGAGTTTTCCACCTGGTACATATCCTCAGATCCCAACATTAATAAATTTATCAAGTACTTGATAATCTTCCTC?
tortugensis  CATCACTGAATTTTCCATGTGGTATATGTCCTCAGACCCC??TATTAACAAATTCATTAAATACTTAACAACCTTCCTAA
transversus  CATTGTCGAATTTACCATCTGATATATGTCCTCAGACCCTAACATTAACAAGTTCATTAAATACTTAACAACCTTTCTAA
triseriatus  TATTACTGAGTTCTCCATCTGATACATGTCCTCAGACCCAAATATCAACAAATTTATTAAATATCTAATAGCCTTTCTAA
unicolor     CATTGTTGAATTTTCCATCTGGTACATATCCGCAGACCCAAATATTAACAAGTTCATTAAATACCTAATAACCTTTTTAA
vegrandis    CATTGTTGAATTTTCCATCTGGTACATATCCTCAGACCCAAATATTAACAAGTTCATTAATTACCTAATAACCTTTTTAA
viridis      --------------------------------------------------------------------------------
willardi     CATTCTACAATTCTCCATTTGATACATAGCCTCAGACCCAAATATCAACAAATTCATTAAATATCTAATAACCTTTCTAA
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             401      410        420        430        440        450        460        470        480
adamanteus   TCACAATGATAATTATCATTACAGCCAACAACATGTACCAACTCTTCATCGGTTGAGAAGGAGTAGGAATCATGTCA
aquilus      TAATCACAATAATAATCATCATTACAGCTAACAACATGTACCAACTCTTCATCGGTTGAGAAGGAGTAGGAATCATGTCA
atrox        TCACAATGATAATTATCATTACAGCCAACAACATGTACCAACTCTTCATCGGTTGAGAAGGAGTAGGAATCATGTCA
basiliscus   TCACAATGATGATTATCATTACAGCCAACAATATGTATCAACTCTTTATTGGTTGAGAAGGAGTAGGAATCATGTCA
bilineatus   ????????????????????????????????????????????????????????????????????????????????
blomhoffii   ????????????????????????????????????????????????????????????????????????????????
catalinensis????????????????????????????????????????????????????????????????????????????????
catenatus    TCGCAATAATAATTATTATCACAGCCAACAACATATATCAATTATTCATCGGCTGAGAAGGAGTAGGAATCATGTCA
cerastes     ????????????????????????????????????????????????????????????????????????????????
contortrix   TTACAATAATAATCATCATTACAGCCAATAACATATATCAACTCTTTGTAGGCTGAGAAGGAGTAGGAATCATGTCA
durissus     TCACAATAATAGTTATCATTACAGCCAACAATGTGTACCAACTATTTATCGGCTGAGAAGGAGTAGGAATCATGTCA
enyo         ????????????????????????????????????????????????????????????????????????????????
horridus     TCACAATAATAATCATCATTACAGCTAACAACATATACCAACTCTTTATTGAC-----------------------
intermedius  ????????????????????????????????????????????????????????????????????????????????
lepidus      TCACAATAATAATCATCATTACAGCCAATAACATGTACCAGCTATTTATCGGTTGAGAAGGAGTAGGAATCATGTCA
miliarius    TCGCAATATTAATTATTATTACAGCCAACAACATATATCAACTATTCATCGGT-----------------------
mitchelli    ????????????????????????????????????????????????????????????????????????????????
molossus     TCACAATAATAATTATCGTTACGGCCAATAACATATACCAACTCTTTATCGGCTGAGAAGGAGTAGGAATCATGTCA
muta         ????????????????????????????????????????????????????????????????????????????????
piscivorus   TTACAATAATAATTATCATTACAGCCAATAACATATACCAACTCTTTATGGGGTGAGAAGGAGTAGGAATCATGTCA
polystictus  TCACAATAATAATCATCATTACAGCTAATAACATATACCAACTCTTTATCGGCTGAGAAGGAGTAGGAATCATGTCA
pricei       TTACAATAATAATCATTATTACAGCTAATAATATGTACCAACTCTTTATCGGCTGAGAAGGAGTAGGAATCAGTGCA
pusillus     T?ACAAT?ATAAT?AT?ATTACAGC?AATAA?ATGTACCAACTCTT?ATCGGC-----------------------
ravus        TTACAATAATAATCATCATTACAGCCAACAACATGTACCAACTTTTGCTCGGTTGAGAAGGAGTAGGAATCATGTCA
ruber        TCACAATGATAATTAT?ATTACAGCCAATAACATGTACCAACTCTTCATCGGCTGAGAAGGAGTAGGAATCATGTCA
scutulatus   ----------------------------------------------------------------------------
stejnegeri   ----------------------------------------------------------------------------
tigris       ???????TATAATCATCATTACAGCCAATAACATGTACCAGCTCTTTATCGGTTGAGAAGGAGTAGGAATCATGTCA
tortugensis  TCACAATGATAATTATTATTACAGCCAACAACATGTATCAACTCTTCATCGGCTGAGAAGGAGTAGGAATCATGTCA
transversus  TTACAATAATAATTATCATTACAGCTAACAATGTGTACCAACTCTTTATCGGCTGAGAAGGAGTAGGAGT-------
triseriatus  TCACAATAATAATCATCATTACAGCTAACAACATATACCAACTCTTCATCGGTT-----------------------
unicolor     TCACAATAATAGTTATCATTACAGCCAACAACGTATACCAACTATTTATCGGCTGAGAAGGAGTAGGAATCATGTCA
vegrandis    TCACAATAATAGTTATCATTACAGCCAACAATGTGTACCAACTATTTATCGGCTGAGAAGGAGTAGGAATCATGTCA
viridis      ----------------------------------------------------------------------------
willardi     TTACAATAATAATCATTATTACAGCTAATAATATGTACCAACTCTTTATCGGCTGAGAAGGAGTAGGAATCATGTCA
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12S/tRNA^{val}/16S data set

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            1        10        20        30        40        50        60        70        80
adamanteus  GCCTAGCCGTAACATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGT-A-TACTTAAAACTTAAAAGACTTG
aquilus     GCCTAACCGTAATATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGTTA-CACTTAAAACTTAAAAGACTTG
atrox       GCCTAGCCGTAACATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
basiliscus  GCCTAGCCGTAACATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TTCTTAAAACTTAAAAGACTTG
bilineatus  --------------------------------------------------------------------------------
blomhoffii  ????????????????????????????????????????????????????????????????????????????
catalinensisGCCTAGCCGTAACATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
catenatus   GCCTAGCCGTAACATACAATTAAACTACTAA-TTGTCCGCCAAACAACTACGAGTAG-TACTTAAAACTTAAAAGACTTG
cerastes    GCCTAGCCATAACCTACAATTAAATCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
contortrix  GCCTAGCCGAAACACACAATTAAATTACCAA-TTGTTCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
durissus    GCCTAGCCGTAACATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
enyo        GCCTAGCCATAACTTACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
horridus    GCCTAACCTTAACATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
intermedius GCCTAACCATAAAATACAATTAAACCACCAAATTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
lepidus     GCCTAACCGTAATATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGTTA-CACTTAAAACTTAAAAGACTTG
miliarius   GCCTAGCCGTAACATACAATTAAACTACCAA-TTGTCCGCCAAACAACTACGAGTTG-CACTTAAAACTTAAAAGACTTG
mitchelli   GCCTAGCCGTAACATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
molossus    GCCTAACCGTAATATACAATTAAACCACCGA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
muta        --------------------------------------------------------------------------------
piscivorus  GCCTGGCCGTAACACACAATTAAATTACCAA-TTGTTCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
polystictus GCCTAGTCGTAACATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
pricei      GCCTAACCGTAACATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
pusillus    GCCTAGCCGTAATATACAATTAAACCACTAA-TTGTCCGCCAAACAACTACGAGTAA-TACTTAAAACTTAAAAGACTTG
ravus       GCCTAGCCGTAATATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGCTAATGCTTAAAACTTAAAAGCATTG
ruber       GCCTAGCCGTAACATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGTTA-CACTTAAAACTTAAAAGACTTG
scutulatus  GCCTAGCCGTAACATACAATTAAACCACCAA-TTGTCCGCCGAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
stejnegeri  --------------------------------------------------------------------------------
tigris      GCCTAGCCGTAACATACAATTAAATCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
tortugensis GCCTAGCCGTAACATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
transversus GCCTAACCATAAAATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
triseriatus GCCTAACTACAATATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGCTA-TACTTAAAACTTAAAAGACTTG
unicolor    GCCTAGCCGTAACATACAATTAA-CCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
vegrandis   GCCTAGCCGTAACATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
viridis     GCCTAGCCGTAACATACAATTAAACCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
willardi    GCCTAGCCGTAACATACAATTAAATCACCAA-TTGTCCGCCAAACAACTACGAGTTA-TACTTAAAACTTAAAAGACTTG
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             81        90        100       110       120       130       140       150       160
adamanteus   ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAGTAACCGATAATCCACGATTAACCCAGCCCCCTCTGGCCTAACAG
aquilus      ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAGTAACCGATAATCCACGATTAACCCAGCCCCCTCTGGCCTAACAG
atrox        ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAATAACCGATAATCCACGATTAACCCAGCCCCCTCTGGCCTAACAG
basiliscus   ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCCAATAACCGATAATCCACGATTAACCCAACCCCCTCTAGCCTAACAG
bilineatus   --------------------------------------------------------------------------------
blomhoffii   ????????????????????????????????????????????????????????????????????????????
catalinensisACGGTGCTTCACTACGCCCTAGAGGAGCCTGTCTAATAACCGATAATCCACGATTAACCCAGCCCCCTCTAGCCCAACAG
catenatus    ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAGCAACCGATAATCCACGATTAACCCAGCCTCCTCTGGCCTAACAG
cerastes     ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCCAGTAACCGATAATCCACGATTAATCCAGCCCCCTCTAGCCTAACAG
contortrix   ACGGTACTTCACCACACCCTAGAGGAGCCTGTCTAATAACCGATAATCCACGATTAACCCAACCCCCTCTTGCC-AACAG
durissus     ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCCAGTAACCGATAATCCACGATTAACCCAACCCCTTCTAGCCTGACAG
enyo         ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAATAACCGATAATCCACGATTAACCCAACCCCCTCTGGCCCAACAG
horridus     ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAGTAACCGATAATCCACGATTAACCCAGCCCCTCCTGGCCTAACAG
intermedius  ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAGTAACCGATAATCCACGATTAACCCAGCCCCCTCTCGCCCAACAG
lepidus      ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAGTAACCGATGATCCACGATTAACCCAGCCCCCTCTGGCCCAACAG
miliarius    ACGGTGCTTCACCACACCCTAGAGGAGCCTGTCTAGTAACCGATAACCCACGATTAACCCAACCCCCCCTAGCCTGACAG
mitchelli    ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAGTAACCGATAATCCACGATTAACCCAGCCCCCTCTGGCCTAACAG
molossus     ACGGTGCTTCAC-ACGTCCTAGAGGAGCCTGTCCAATAACCGATAATCCACGATTAACCCAACCCCCTCTAGCCTAACAG
muta         --------------------------------------------------------------------------------
piscivorus   ACGGTACTTCACCACGCCCTAGAGGAGCCTGTCCAATAACCGATAATCCACGATTAACCCAACCCCCTCTTGCC-AACAG
polystictus  ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAATAACCGATAATCCACGATTAACCCAACCCCTTCTAGCCTAACAG
pricei       ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAGTAACCGATAATCCACGATTAACCCAGCCCCCTCTCGCCCAACAG
pusillus     ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAGTAACCGATAATCCACGATTAACCCAGCCCCCTCTGGCCTAACAG
ravus        ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAGTAACCGATAATCCACGATTAACCCAGCCCCCCCTAGCCTAACAG
ruber        ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAATAACCGATAATCCACGATTAACCCAGCCCCCTCTAGCCCAACAG
scutulatus   ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAGTAACCGATAATCCACGATTAACCCAGCCCCCTCTGGCCCAACAG
stejnegeri   --------------------------------------------------------------------------------
tigris       ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAGTAACCGATAATCCACGATTAACCCAACCCCCTCTAGCCTGACAG
tortugensis  ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAATAACCGATAATCCACGATTAACCCAGAAAAATATGGCCTAACAG
transversus  ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAGTAACCGATAATCCACGATTAACCCAGCCCCCTCTCGCCCTACAG
triseriatus  ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAGTAACCGATGATCCACGATTAACCCAGCCCCCTCTAGCCTAACAG
unicolor     ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCCAGTAACCGATAATCCACGATTAACCCAACCCCTTCTAGCCTAACAG
vegrandis    ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCCAGTAACCGATAATCCACGATTAACCCAACCCCTTCTAGCCTGACAG
viridis      ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTAGTAACCGATAATCCACGATTAACCCAGCCCCCTCTGGCCCAACAG
willardi     ACGGTGCTTCACCACGCCCTAGAGGAGCCTGTCTGGTAACCGATAATCCACGATTAACCCAGCCCCCCCAAGCCTAACAG
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             161     170       180       190       200       210       220       230       240
adamanteus   TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTAAGCCAAATAGCATC-ACACTTAAACGACAGGTCG
aquilus      TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTGAGCTAAATAGCACC-ACACTTAAACGACAGGTCG
atrox        TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTAAGCCAAATAGCACC-ACACTTAAACGACAGGTCG
basiliscus   TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAAGAAAGTGAGCCAAATAGCACT-ACACTCAAACGACAGGTCG
bilineatus   ------------------------------------------------------------------------------
blomhoffii   ??????????????????????????????????????????????????????????????????????????????
catalinensisTCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGTAATAAAGTAAGCCAAATAGCACT-ACACTTAAACGACAGGTCG
catenatus    TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTAAGCCAAACAGTATTTTCCCTAAAACGACAGGTCG
cerastes     TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTGAGCCAAATAGCACC-ACACTAAAACGACAGGTCG
contortrix   TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATATAGTGAGCTAAATAGTACT-TCACTAAAACGACAGGTCG
durissus     TCTATATACCGCCGTCGCCAGCTTACCTTGTGAAAGAAAGAAAGTGAGCTAAATAGCACC-ACACTAAAACGACAGGTCG
enyo         TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTGAGCCAAACAGCACC-ACACTTAAACGACAGGTCG
horridus     TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTGAGCTAAACAGCACC-ACACTTAAACGACAGGTCG
intermedius  TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTGAGCCAAATAGCACT-ACACTTAAACGACAGGTCG
lepidus      TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTGAGCTAAATAGCACT-ACACTTAAACGACAGGTCG
miliarius    TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTGAGCTAAATAGTATA-CCACTAAAACGACAGGTCG
mitchelli    TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTAAGCCAAATAGCAC--ACACTTAAACGACAGGTCG
molossus     TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAAAAAAGTGAGCTAAATAGCACC-ACACTCAAACGACAGGTCG
muta         ------------------------------------------------------------------------------
piscivorus   TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTGAGCTAAATAGTACCAACACTAAAACGACAGGTCG
polystictus  TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTGAGCCAAACAGCCCCTACACTAAAACGACAGGTCG
pricei       TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTGAGCCAAATAGTACC-GCACTTAAACGACAGGTCG
pusillus     TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTGAGCTAAATAGCCCC-ACACTTAAACGACAGGTCG
ravus        TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTGAGCTAAACAGTACC-ACACTTAAACGACAGGTCG
ruber        TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTAAGCCAAATAGCACT-ACACTTAAACGACAGGTCG
scutulatus   TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTAAGCCAAATAGTACA-ACACTTAAACGACAGGTCG
stejnegeri   ------------------------------------------------------------------------------
tigris       TCTATATACCGCCGTCGCCAGCCTACCTTGTAAAAGAAATAAAGTAAGCCTAACAGTATC-ACGCTTAAACGACAGGTCG
tortugensis  TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTAAGCCAAATAGCACT-ACACTTAAACGACAGGTCG
transversus  TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAATTAAAGTGAGCCAAATAGCACT-ACACTTAAACGACAGGTCG
triseriatus  TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTGAGCTAAATAGTACC-ACACTTAAACGACAGGTCG
unicolor     TCTATATACCGCCGTCGCCAGCTTACCTTGTGAAAGAAAGAAAGTGAGCTAAATAGCACC-ACACTAAAACGACAGGTCG
vegrandis    TCTATATACCGAAGTCGCCAGCTTACCTTGTGAAAGAAAGAAAGTGAGCTAAATAGCACC-ACACTAAAACGACAGGTCG
viridis      TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTAAGCCAAATAGTACC-ACACTCAAACGACAGGTCG
willardi     TCTATATACCGCCGTCGCCAGCTTACCTTGTAAAAGAAATAAAGTGAGCCAAATAGCACC-ACACTTAAACGACAGGTCG
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             241     250       260       270       280       290       300       310       320
adamanteus   AGGTGTAACTAATGAGAGGG-ACTAAGATGGGCTACATTCTCTCAACTGAGGATACGAACAACACTATGAAATTAGTGTT
aquilus      AGGTGTAACTAATGAGAGGG-ACTAAGATGGGCTACATTCTCTTACCCGAGAATACGAACAATACTATGAAATTAGTGTT
atrox        AGGTGTAACTAATGAGGGGG-ACTAAGATGGGCTACATTCTCTAAATAGAGAATACGAACAACACTATGAAATTAGTGTT
basiliscus   AGGTGTAACTAATGAGAGGG-ACTAAGATGGGCTACATTCTCT-AACCGAGAATACGAACAACACTATGAAATTAGTGTT
bilineatus   --------------------------------------------------------------------------------
blomhoffii   ????????????????????????????????????????????????????????????????????????????
catalinensisAGGTGTAACTAATGAGGGGG-ACTAAGATGGGCTACATTCTCTAAACCGAGAATACGAACAACACTATGAAATTAGTGTT
catenatus    AGGTGTAACTAATGAGGAGG-ACTAAGATGGGCTACATTCTCCTAACCGAGAATACGAACAATACTATGAAATTAGTATT
cerastes     AGGTGTAACTAATGAGGGGG-ACTAAGATGGGCTACATTCTCCTGACCGAGAACACGAACAACACTGTGAAATCAGTGTT
contortrix   AGGTGTAACTAATGAAGGG---TTAAGATGG-CTACATTCTCC-AACCGAGAACACGAACAATACTATGAAATTAGTACT
durissus     AGGTGTAACTAATGAAGAGG-ACTAAGATGGGCTACATTCTCT-AACCGAGAACACGAACAACACTATGAAATTAGTGTT
enyo         AGGTGTAACTAATGAGGGGGGACTAAGATGGGCTACATTCTCCCAACCGAGAATACGAACAATACTATGAAATTAGTATT
horridus     AGGTGTAACTAATGGGGGGG-ACTAAGATGGGCATCATTCTCTTAACCGAGAACACGAACAACACTGTGAAATTAGTGTT
intermedius AGGTGTAACTAATGAGGGGG-ACTAAGATGGGCTACATTCTCT-ATCCGAGAATACGAACAATACTATGAAATTAGCATT
lepidus      AGGTGTAACTAATGAGGGGG-ACTAAGATGGGCTACATTCTCTTGTCCGAGAATACGAACAATACTATGAAATTAGTGTT
miliarius    AGGTGTAACTAATGGGAGGG-ATTAAGATGGGCTACATTCTCCTTTCTGAGAA-ACGAACAATACTATGAAACTAGTATT
mitchelli    AGGTGTAACTAATGAGGGGG-ACTAAGATGGGCTACATTCTCTCAACTGAGAATACGAACAACACTATGAAATTAGTGTT
molossus     AGGTGTAACTAATGAGGGGG-ACTAAGATGGGCTACATTCTCT-AACCGAGAATACGAACAACACTATGAAATTAGTGTT
muta         --------------------------------------------------------------------------------
piscivorus   AGGTGTAACTCATGAAGGGG--CTAAGATGGGCTACATTCTCC-AACCGAGAAAACGAACAACACTATGAAACTAGTCTT
polystictus  AGGTGTAACCAATGAAGGGG-GTTAAGATGGGCTACATTCTCCTGACCGAGAACACGAACAACACTATGAAATTAGTGTT
pricei       AGGTGTAACTAATGAGGGGG-ACTAAGATGGGCTACATTCTCT-ACCCGAGAATACGAACAATACTATGAAGCTAGTATT
pusillus     AGGTGTAACTAATGGGGGGG-ACTTAGATGGGCTACATTCTCTTGTCCGAGAATACGAACAACACTATGAAATAAGTGTT
ravus        AGGTGTAACTAATGAGGGGG-ACTAAGATGGGCTACATTCTCTTGACCGAGAATACGAACAATACTATGAAATTGGTATT
ruber        AGGTGTAACTAATGAGGGGG-ACTAAGATGGGCTACATTCTCTAAACCGAGAATACGAACAACACTATGAAATTAGTGTT
scutulatus   AGGTGTAACTAATGAGGGGG-ACCAAGATGGGCTACATTCTCCTAACTGAGAACACGGACAACACTATGAAATTAGTGTT
stejnegeri   --------------------------------------------------------------------------------
tigris       AGGTGTAACTAATGAGTGGG-ACTAAGATGGGCTACATTCTCTCGACTGAGAATACGAACAACACTATGAAATTAGTGTT
tortugensis  AGGTGTAACTAATGAGGGGG-ACTAAGATGGGCTACATTCTCTAAATAGAGAATACGAACAACACTATGAAATTAGTGTT
transversus  AGGTGTAACTAATGAGGGGG-ACTAAGATGGGCTACATTCTCT-ATCCGAGAATACGAACAATACTATGAAATTAGCATT
triseriatus  AGGTGTAACTAATGAAGGGG-CCTAAGATGGGCTACATTCTCCTATCCGAGAATACGAACAATACTATGAAATTAGTGTT
unicolor     AGGTGTAACTAATGAAGGGG-ACTAAGATGGGCTACATTCTCT-AACCGAGAACACGAACAACACTATGAAATTAGTGTT
vegrandis    AGGTGTAACTAATGAAGAGG-ACTAAGATGGGCTACATTCTCT-AACCGAGAACACGAACAACACTATGAAATTAGTGTT
viridis      AGGTGTAACTAATGAGGGGG-ACCAAGATGGGCTACATTCTCCTAACCGAGAACACGAACAACACTATGAAACTAGTGTT
willardi     AGGTGTAACTAATGAGGGGG-ATTAAGATGGGCTACATTCTCT-GACCGAGAATACGAACAACACCATGAAATTAGTGTT
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             321      330        340        350        360        370        380        390        400
adamanteus   TAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAACACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
aquilus      TAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAACACTTAACTGAACATAACGCAATGAAGTGCGCACACACCGCCCGT
atrox        TAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAACACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
basiliscus   TAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAACACTTAACTGAACATAACGCAATGAAGTGCGCACACACCGCCCGT
bilineatus   ----------------------------------------------------------------------------
blomhoffii   ????????????????????????????????????????????????????????????????????????????
catalinensisTAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAACACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
catenatus    TAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAATACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
cerastes     CAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAACACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
contortrix   TAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAAAGCTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
durissus     TAAAGGCGGATTTAGCAGTAAGTTAA-GAATAAAACACCTAACTGAACATAACGCAATGAAGTGCGCACACACCGCCCGT
enyo         TAAAGGCGGATTTAGCAGTAAGATAA-GAATAGAACACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
horridus     TAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAATACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
intermedius  AAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAATACTTAACTGAACATAACGCAATGAAGTGCGCACACACCGCCCGT
lepidus      CAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAACACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
miliarius    TAAAGACGGATTTAGCAGTAAGATAA-GAATAAAATACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
mitchelli    CAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAATACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
molossus     TGAAGGCGGATTTAGCAGTAAGATAA-GAATAAAACACTTAACTGAACATAACGCAATGAAGTGCGCACACACCGCCCGT
muta         ----------------------------------------------------------------------------
piscivorus   TAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAAAGCTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
polystictus  CAAAGGCGGATTTAGCAGTAAGATAA-GAATAGAACACTTAACTGAACACAACGCAATGAAGTGCGTACACACCGCCCGT
pricei       TAAAGGCGGATTTAGCAGTAAGATAA-GGATAAAATACTTAACTGAACATAACGCAATGAAGTGCGCACACACCGCCCGT
pusillus     TAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAACACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
ravus        CAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAACACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
ruber        TAAAGGCGGATTTAGCAGTAAGATAAAGAATAAAATACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
scutulatus   CAAAGACGGATTTAGCAGTAAGATAA-GAATAAAATACTTAACTGAACATAACGCAATGAAGCGCGCACACACCGCCCGT
stejnegeri   ----------------------------------------------------------------------------
tigris       TAAAGGCGGAATTAGCAGTAAGATAA-GAATAAAATACTTAACTGAATATAACGCAATGAAGTGCGTACACACCGCCCGT
tortugensis  TAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAACACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
transversus  AAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAATACTTAACTGAACATAACGCAATGAAGTGCGCACACACCGCCCGT
triseriatus  CAAAGGAGGATTTAGCAGTAAGATAA-GAATAAAACACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
unicolor     TAA-GGCGGATTTAGCAGTAAGTTAA-GAATAAAACACCTAACTGAACATAACGCAATGAAGTGCGCACACACCGCCCGT
vegrandis    TAAAGGCGGATTTAGCAGTAAGTTAA-GAATAAAACACCTAACTGAACATAACGCAATGAAGTGCGCACACACCGCCCGT
viridis      AAAAGGCGGATTTAGCAGTAAGATAA-GAATAAAACACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
willardi    TGAAGGCGGATTTAGCAGTAAGATAA-GAATAGAATACTTAACTGAACATAACGCAATGAAGTGCGTACACACCGCCCGT
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             401     410       420       430       440       450       460       470       480
adamanteus   CACCCCGTCCACCACCAC-AATACACATTTAATTAAACCAACC--AAAAACA-TAAAC-CAGGGCAAGTCGTAACATGGT
aquilus      CACCCC---TGTCACCAC-AACACATCTTTAAT-AAACCGACCAAAAAAACA-C-AAC-CAGGGCAAGTCGTAACATGGT
atrox        CACCCC---TGCCACCAC-AACACATCTTTAATTAAACCAAC--AAAAAACA-TAAAC-CAGGGCAAGTCGTAACATGGT
basiliscus   CACCCC---TGCCACCAC-AACACATCTTTAACTAAACCAACC-AAAAAACA-CAAAC-CAGGGCAAGTCGTAACATGGT
bilineatus   ----------------------------------------------------------------------------
blomhoffii   ????????????????????????????????????????????????????????????????????????????
catalinensisCACCCC---TGCCACCAC-AACACATCTTTAATTAAACCAAC-AAAAGAACA-CAAAC-CAGGGCAAGTCGTAACATGGT
catenatus    CACCCC---TGCTAAAAC-AACACATAATTAAATAAACCA-CCAAAAACACT-TAAAC-CAGGGTAAGTCGTAACATGGT
cerastes     CACCCC---TGCCACCACTAACACACATTTAAT-AAACCAATC--AAAACCA-CAAAC-CAGGGCAAGTCGTAACATGGT
contortrix   CATCCC---TGCCACCAC-AATGTA-AACTTAATAAACCTACG-AAAAAA-A-TCAAA-CAGGGCAAGTCGTAACATGGT
durissus     CACCCC---TGCCACCAC-AACATATCTTTAAT-AAACCAACC--AAAAACA-TAAAC-CAGGGTAAGTCGTAACATGGT
enyo         CACCCC---TGCCACCAC-AACACATCTTTAATTAAACCAACC-AAACAACA-CAAAT-CAGGGCAAGTCGTAACATGGT
horridus     CACCCC---TGCTACTAC-AACACACCTTTTAT-AAACCAATC-AGAAAACA--AAAC-CAGGGCAAGTCGTAACATGGT
intermedius  CACCCC---TGCCACCAC-AAAATACACTTTTATAAAC-AACCAAAAAAATT-AAAAT-CAGGGCAAGTCGTAACATGGT
lepidus      CACCCC---TGTCACCAC-AATACATCTTTAAT-AAACCAACC-GAAATACA-CAAAC-CAGGGCAAGTCGTAACATGGT
miliarius    CACCCC---TGCTACCAC-AACACACAACTTTATAAACCA-CCA-TAAAACA-TAAAC-CAGGGTAAGTCGTAACATGGT
mitchelli    CACCCC---TGCCACCACTAATCCATCCTTAAT-AAACCAACC--AAAAACA-TAAAC-CAGGGCAAGTCGTAACATGGT
molossus     CACCCC---TGCCACCACTAACA-ATCTTTAATTAAACCAACC--AAAAACA-TAAAC-CAGGGCAAGTCGTAACATGGT
muta         ----------------------------------------------------------------------------
piscivorus   CATCCC---TGCCACCAC-AACGTA-AACTTAATAAACCAAGTAAAATAA-A-CCAAA-CAGGGCAAGTCGTAACATGGT
polystictus  CACCCC---TGCCAAAAC-AACACATCATTTAT-AAACCAAC--AAAAAACA-CTAAC-CAGGGCAAGTCGTAACATGGT
pricei       CACCCC---TGCCACCAC-GATACACTTTATAAAAAACCA----GAAAATTA--AAAC-CAGGGCAAGTCGTAACATGGT
pusillus     CACCCC---TGCCACCAC-AACACATCTTTAAT-AAAC-AACC-AAAAAACA-CAAAC-CAGGGCAAGTCGTAACATGGT
ravus        CACCCC---TGCCACCAC-AACCCTTTTTTAATTAAACCAACC--AAAAACA-TAAAC-CAGGGCAAGTCGTAACATGGT
ruber        CACCCC---TGCCACCAC-AACACATCTTTAATTAAACCGAAC-AAAGAACA-TAAAC-CAGGGCAAGTCGTAACATGGT
scutulatus   CACCCC---TGCTACCAC-AACACACATTTAAT-AAACCAACC--AAAAACA-TAAAC-CAGGGCAAGTCGTAACATGGT
stejnegeri   ----------------------------------------------------------------------------
tigris       CACCCC---TGCCACCAT-AACACATATTTAAT-AAACTGAC--AAAAAACATTAAAC-CAGGGCAAGTCGTAACATGGT
tortugensis  CACCCC---TGCCACCAC-AACACATCTTTAATTAAACCAAC--AAAAAACA-TAAAC-CAGGGCAAGTCGTAACATGGT
transversus  CACCCC---TGCCACCAC-AACACACACTTTAATAAAT-GACCAAAAAATTA-TAAAC-CAGGGCAAGTCGTAACATGGT
triseriatus  CACCCC---TGTCACCAC-AACATATCTTTAATTAAACCAACC--AAAAACA-TAAAC-CAGGGCAAGTCGTAACATGGT
unicolor     CACCCC---TGCCACCAC-AACATATCTTTAAT-AAACCAACC--AAAAACA-TAAAC-CAGGGTAAGTCGTAACATGGT
vegrandis    CACCCC---TGCCACCAC-AACATATCTTTAAT-AAACCAACC--AAAAACA-TAAAC-CAGGGTAAGTCGTAACATGGT
viridis      CACCCC---TGCCACCAC-AACACATATTCAAT-AAACCAACC--GAAAACA-CAAAC-CAGGGTAAGTCGTAACATGGT
willardi     CACCCC---TGCCACCAC-AACACATCTTTAAT-AAACCAACC--AAAAACA-TAAACTCAGGGCAAGTCGTAACATGGT
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             481     490       500       510       520       530       540       550       560
adamanteus   AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-CAAAGCAGTCGACCTACACTCGAACGATATTA-AA
aquilus      AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAG-CAAAGCACTCGACTTACACTCGAACGATATTA-CA
atrox        AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-AAAAGCACTCGACCTACACTCGAACGATATTA-AA
basiliscus   AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-CAAAGCACTCGACTTACACTCGAACGATATTA-AA
bilineatus   ----------------------------------------------------------------------------
blomhoffii   ????????????????????????????????????????????????????????????????????????????
catalinensisAAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-AAAAGCACTCGACCTACACTCGAACGATATTA-AA
catenatus    AAGCGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-CAAAGCACTCGACTTACACTCGAGCGATATTA-CA
cerastes     AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-CAAAGCACTCGACCTACACTCGAACGATATTA-AA
contortrix   AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTACA-CAAAGCACTCGACCTACACTCGAACGACATTAACA
durissus     AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAAACAAAGCACTCGACCTACGCTCGAACGATATTA-AA
enyo         AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-CAAAGCACTCGACCTACACTCGAACGATATTA-AA
horridus     AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-CAAAGCACTCGACTTACACTCGAACGATATTA-AA
intermedius AAGTGTACTGGAAAGTGTACTTTAGAAACAAAAAGTAGCTTAAT-TAAAGCACTCGACTTACACTCGAACGATATTA-CA
lepidus      AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-CAAAGCACTCGACT-ACATTCGAACGATATTA-CA
miliarius    AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-CAAAGCACTCGACCTACACTCGAACGATATTA-CA
mitchelli    AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-CAA-GCACTCGACCTACACTCGAACGATATTA-AA
molossus     AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-AAAAGCACCCGACTTACACTCGTGCGATATTA-AA
muta         ----------------------------------------------------------------------------
piscivorus   AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTACA-CAAAGCACTCGACCTACACTCGAACGACATTAATA
polystictus AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-CAAAGCACTCGACTTACACTCGAATGATATTA-CA
pricei       AAGTGTACTGGAAAGTGTACTT-AGAAACAAAAAGTAGCTTAAA-CAAAGCACTCGGCTTACACTCGAACGATATTA-CT
pusillus     AAGTGTACTGGAAAGTGCACTT-AGAACCAAAAAGTAGCTTAAA-CAAAGCACTCGACCTACACTCGAACGATATTA-CA
ravus        AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-CAAAGCACTCGACTTACACTCGAACGATATTC-TA
ruber        AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAATT-AAGCACTCGACCTACACTCGAACGATATTAAAT
scutulatus   AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-CAAAGCACTCGACCTACACTCGAACGATATTA-AA
stejnegeri   ----------------------------------------------------------------------------
tigris       AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-CAAAGCACTCGACCTACACTCGAACGATATTT-AA
tortugensis  AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAAATAAAGCGCTCGACCTACACTCGAACGATATTA-AA
transversus  AAGCGTA------------------------------------------------------------------------
triseriatus  AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-CAAAGCACTCGACTTACACTCGAGCGATATTT-CA
unicolor     AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAAACAAAGCACTCGACCTACGCTCGAGCGATATTA-AA
vegrandis    AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAAACAAAGCATTCGACCTACGCTCGAACGATATTA-AA
viridis      AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-CAAAGCACTCGACCTACACTCGAACGATATTA-AA
willardi     AAGTGTACTGGAAAGTGCACTT-AGAAACAAAAAGTAGCTTAAA-CAAAGCCCTCGACTTACACTCGAACGATATTA-GA
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             561     570       580       590       600       610       620       630       640
adamanteus   CTAATCTTTTTGAGCTGACCTAACAAC-AAACCACAAATATACCTACACAGAATTAAACAAATCATTT-GACCAACCTAG
aquilus      TTAATCTTTTTGAGCTGACCGAACAAC-AAACCACAAATATACCCT-ACTGAATTAAACAAATCATTT-GACCAGCCCAG
atrox        TTAATCTTTTTGAGCTGACCTAACAAC-AAACCACAAATATACACT-ACTAAATTAAACAAATCATTT-GACCTACCCAG
basiliscus   TTAATCTTTTTGAGCTGACCAGACAAC-AAATCACAAACATACCCT-ACTGAG-AAAACAAAACATTT-GACCAACCTAG
bilineatus   --------------------------------------------------------------------------------
blomhoffii   ????????????????????????????????????????????????????????????????????????????
catalinensisTTAATCTTTTTGAGCTGACCCAACAAC-AAATCACAAATATATCCT-ACCAAA-TAAACAAATCATTT-GACCTACCTAG
catenatus    TAAATCTTTTTGAGCTGATCGAACAAC-GAACCACAAACATACCAC-AATAAAC-AAACAAATCATTT-GACCTACCCAG
cerastes     TTAATCTTTTTGAGCCGACCATACAACTAAACCACAAACATACTTT-ACTGAA-AAAACAAACCATTT-GACCAACCTAG
contortrix   TTAATCTTTTTGAGCTGACTAAACGACTTAACCACAAATATACCTT-ACCAAAC-AAACAAATCATTT-GCCCCACCTAG
durissus     TTAATCTTTTTGAGCTGACCGAACAAC-AAACCACAAATATATTTC-ACCAAATAAAACAAATCATTT-GACCATCCTAG
enyo         TTAATCTTTTTGAGCTGACCTAACAAC-GAACCACAAATATACTTT-ACTGAGC-AAACAAACCATTT-GACCAACCTAG
horridus     TTAATCTTTTTGAGCTGACCAGACAAC-AAACCACAAACATACCCT-ACTAAAC-AAACAAATCATTT-GACCAGCCTAG
intermedius  TTAATCTTTTTGAGCTGACATAACAACTAAGCCACAAATATACATT-ATTGAA--AAACAAAACATTT-GACCAACCCAG
lepidus      TTAATCTTTTTGAGCTGACCGAACAAC-GAACCACAAATATACCCT-ACCAAATTAAACAAATCATTT-GACCTACCCAG
miliarius    TTAATCTTTTTGAGCTGATTAAACAAC-AAACTACAAATATACTAC-ACAAAAT-AAACAAATCATTT-GACCCACCCAG
mitchelli    TTAATCTTTTTGAGCTGACCTGACAACTAAACCACAAATATACCCT-ACTGAATAAAACAAATCATTTTGACCAACCTAG
molossus     TTAATCTTTTTGAGCTGACCAAACAAC-AAATCACAAATATACCCT-ACTGAA-AAAACAAACCATTT-GACCAACCTAG
muta         --------------------------------------------------------------------------------
piscivorus   TTAATCTTTTTGAGCTGACTAAACTACT-AACCACAAATATACCTT-ACCGAAC-AAACAAACCATTT-GCCCCGCCCAG
polystictus  TTAATCTTTTTGAGCCGACTTAACAATCAAACCGCAAATATACTCT-ACTGAA-AAAACAAAGCATTT-GACCTACCTAG
pricei       TTAATCTTTTTGAGC-GGTATAACAACTAAATCACAAATATACTTT-ACCGAAA-AAACAAACCATTT-GACCAACCCAG
pusillus     TTAATATTTTTGAGCTGACCGAACAAC-AGACCACAAACATATCCT-ACTAAAT-AAACAAATCATTT-GACCCACCCAG
ravus        TTAATCTTTTTGAGCTGACCAAACAAC-AAACCACAAATATACCCT-ACTAAAT-AAACAAATCATTT-GACCAACCTAG
ruber        TAAATCCTTTTGAGCTGACCT--TAAC-AA-------------------CAAACTAAACAAATCATTT-GACCTACCCAG
scutulatus   TTAATCTTTTTGAGCTGACCTCACAAC-AAACTACAAGCATACTCT-ACTGAACTAAACAAATCATTT-GACCAACCTAG
stejnegeri   --------------------------------------------------------------------------------
tigris       TTAATCTTTTTGAGCTGACCTAACGA-TAAACCACAAATATACCCT-ACTGAATCAAACAAATCATTT-GACCAACCTAG
tortugensis  TTAATCTTTTTGAGCTGACCTAACAAC-AAACCACAAATATACGCT-AGTAAAGTAAACAAATCATTT-GACCCACCCAG
transversus  --------------------------------------------------------------------------------
triseriatus  TTAATCTTTTTGAGCTGACCGAACAAC-AAACCACAAATATACCTT-ACCAAATTAAACAAAACATTT-GACCCACCCAG
unicolor     TTAATCTTTTTGAGCTGACCGAACAAC-AAACCACAAATATATTTC-ACCAAATAAAACAAATCATTT-GACAATCCTAG
vegrandis    TTAATCTTTTTGAGCTGACCGAACAAC-AAACCACAAATATATTTC-ACCAAATAAAACAAATCATTT-GACCATCCTAG
viridis      TTAATCTTTTTGAGCTGACCTCACAAC-AAACCACAAATATACTTTTACTGAAT-AAACAAATCATTT-GACCAACCTAG
willardi     TTAATCTTTTTGAGCTGACCAAACGACTAAACCACAAACATACTCT-ACTGAAC-AAACAAATCATTT-GACCAACCTAG
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             641     650       660       670       680       690       700       710       720
adamanteus   TAGATGCGATCGAACAGTCAC-AAGTCACACC--AAGTACCGTAAGGAAAC-ACCATT--AAGCAATAAATAGCAAAGAC
aquilus      TAGATGCGATCGAACAGTCAC-AAGTCACAAC-AAAGTACCGCAAGGGAACCACCATC--AAGCAACAAACAGCAAAGAC
atrox        TAGATGCGATCGAACAGTCAC-AAGTCACAAC-AAAGTACCGCAAGGGAAC-ACCATC--AAGCAACAAATAGCAAAGAC
basiliscus   TAGATGCGATCGAACAGATAC-AAGTCACAAC-AAAGTACCGCAAGGGAAC-ACCACTC-AAGCAACAAACAGCAAAGAC
bilineatus   --------------------------------------------------------------------------------
blomhoffii   ????????????????????????????????????????????????????????????????????????????
catalinensisTAGATGCGATCGAACAGTCAC-AAGTCACAAC-AAAGTACCGCAAGGGAAC-ACCATC--AAGCAACAAATAGCAAAGAC
catenatus    TAGATGCGATCGAACAGTTAT-TAGTCACAATCAAAGTACCGCAAGGGAACCACCA-C--AAGCAATGAACAGCAAAGAC
cerastes     TAGATGCGATCGAACAGTCAC-TAGTCATAAC-AAAGTACCGCAAGGGAACCACCATC---AGCAGCAA-CAGCAAAGAT
contortrix   TAGTTGCGATCGAACAGTCAC-AAGTCACAAC-AAAGTACCGCAAGGGAACCACCATT--AAGCATTAAACAGCAAAGAC
durissus     TAGAGGCGATCGAACAGACAC-AAGTCACAAC-AAAGTACCGTAAGGGAAC-ATCATC--AAGCAACAAACAGCAAAGAC
enyo         TAGATGCGATCGAACACTCACAATGTCACAA-AAAAGTACCGCAAGGGAACCACCATT--AAGCAAAAAACAGCAAAGAC
horridus     TAGATGCGATCGAACAGTCAC-AAGTCACAAC-AAAGTACCGCAAGGGAAT-ATCATCT-AAGCAACAAACAGCAAAGAC
intermedius  TAGATGCGATCGAACAGTCAC-ACGTCACAAC-AAAGTACCGTAAGGGAACCACCATC--AAGCAACAAATAGCAAAGAC
lepidus      TAGATGCGATCGAACAGTCAT-AAGTCACAAC-AAAGTACCGCAAGGGAACCACCATC--AAGCAACAAACAGCAAAGAC
miliarius    TAGATGCGATCGAACAGTCAA-AAGTCACAATTAAAGTACCGCAAGGGAAC-ACCAT--GAAGCAACAAACAGCAAGAAT
mitchelli    TAGATGCGATCGAACAGTCACTAAGTCACAAC-AAAGTACCGCAAGGGAAC-ACCAT--AAAGCAACAAATAGCAAAGAC
molossus     TAGATGCGATCGAACAGACAC-AAGTCACAAC-AGAGTACCGCAAGGGAAC-ACCACT-AAAGCAACAAACAGCAAAGAC
muta         --------------------------------------------------------------------------------
piscivorus   TAGTTGCGATCGAACAGCCAC-AAGTCATAAC-AAAGTACCGCAAGGGAAC-ACTATTT-AAGCAGTAAACAGCAAAGAT
polystictus  TAGATGCGATCGAACAGTCACTAAGTCACAAC-AAAGTACCGCAAGGGAACTACCATC--AAGCAACAAACAGCAAAGAC
pricei       TAGATGCGATCGAACAGCCAC-ACGTCACAAC-AAAGTACCGTAAGGGAACCGCCATC--AAGCAATAAACAGCAAAGAC
pusillus     TAGATGCGATCGAACAGTCAC-AAGTCACAAC-AAAGTACCGCAAGGGAACCACCATC--AAGCAACAAACAGCAAAGAC
ravus        TAGATGCGATCGAACAGTCAC-AAGTCATAAC-AAAGTACCGCAAGGGAACCACCATC--AAGCAACAAACAGCAAAGAC
ruber        TAGATGCGATCGAACAGTCAC-TAGTCACAAC-AAAGTACCGCAAGGGAAC-ACCATC--AAGCAACAAATAGCAAAGAC
scutulatus   TAGATGCGATCGAACAGTCAC-AAGTCACAAC-AAAGTACCGCAAGGGAAC-ACCATC--AAGCAACAAACAGCAGAGAT
stejnegeri   --------------------------------------------------------------------------------
tigris       TAGATGCGATCGAACAGTCAC-AAGTCACAAC-AAAGTACCGCAAGGGAAC-ACCATT--AAGCAATAAATAGCAAAGAC
tortugensis  TAGATGCGATCGAACAGTCAC-AAGTCACAAC-AAAGTACCGCAAGGGAAC-ACCATC--AAGCAACAAATAGCAAAGAC
transversus  --------------------------------------------------------------------------------
triseriatus  TAGATGCGATCGAACAGTCAC-AAGTCATAAC-AAAGTACCGCAAGGGAACCACCACC--AAGCAACAAACAGCAAAGAC
unicolor     TAGAGGCGATCGAACAGTCAC-AAGTCACAAC-AAAGTACCGTAAGGGAAC-ATCATT--AAGCAACAAACAGCAAAGAC
vegrandis    TAGAGGCGATCGAACAGACAC-AAGTCACAAC-AAAGTACCGTAAGGGAAC-ATCATC--AAGCAACAAACAGCAAAGAC
viridis      TAGATGCGATCGAACAGCCAC-AAGTCACAAC-AAAGTACCGCAAGGGAAC-ACCATC--AAGCAACAAATAGCAAAGAC
willardi     TAGATGCGATCGAACAGTCAC-AAGTCACAAT-AAAGTACCGCAAGGGAAC-AC-ATTTAAAGCAACAAACAGCAAAGAC
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             721      730        740        750        760        770        780        790        800
adamanteus   TGACCCTTGTACCTTTTGCATCATGGTTTAGCAAG-------------------------CCCCCCCCCCGAAACCGAA
aquilus      TAATCCTTGTACCTTTTGCATCATGGTTTAGCA--AACCACAGGACAAGAAGAATCACAGCCCACCACCCCGAAACCGAA
atrox        TAACCCTTGTACCTTTTGCATCATGGTTTAGCAAGAACAAAAGGACAAGAAGAATCACAGCCCCCCTCCCCGAAATCGAA
basiliscus   TAACCCTTGTACCTTTTGCATCATGGTCTAGCAAGAACACAAGGACAAGAAGAATCACAGCCCTCCACCCCGAAACCGGA
bilineatus   --------------------------------------------------------------------------------
blomhoffii   ????????????????????????????????????????????????????????????????????????????
catalinensisTAACCCTTGTACCTTTTGCATCATGGTTTAGCAAGAACAAAAGGACAAGAAGAATCACAGCCCCCC-CCCCGAAACCGAA
catenatus    TAACCCTTGTACCTTTTGCATCATGGTTTAGCAAGAACACAAGGACAAGAAGAATCATAGCCCTTC-CCCCGAAACCGAA
cerastes     CA--CCTTGTACCTTTTGCATCATGGTTTAGCA-G-ACA-AAGGACA-G-AGAATCAT-G-CCCCCCCCCCGAAACCGAA
contortrix   TAACTCTTGTACCTTTCGCATCATGGTTTAGCAAGAACACAGGGACAAGAAGAATCAAAGCCCCTCCCCCCGAAACCGAA
durissus     TAACCCTTGTACCTTTTGCATCATGGTCTAGCAAGAATATAAGGACAAGAAGAATCATAGCCCCACCCCC-GAAACCGAA
enyo         TAACCCTTGTACCTTTTGCATCATCCTTTAGCTAGAACAAAAGGACAAGAAGAATCATAGCCCAGC-CCCCGAAACCGAA
horridus     TAACCCTTGTACCTTTTGCATCATGGTCTAGCAAGGATATAAGGACAAGGAGAATCACAGCCCCCCCCCCCCGAAACCGAA
intermedius TAACCCTTGTACCTTTTGCATCATGATTCAGCAAGAACACAAGAACAAGAAGAATCACAGCTCTTCCACCCGAAACCGAA
lepidus      TAACCCTTGTACCTTTTGCATTATGGTTTAGCAAG-ATTATAGGACAAGAAGAATCACAGCCCACCCCCC-GAAACCGAA
miliarius    TAACCCCTGTACCTTTTGCATCATGGTTTAGCAAGAACACAAGGACAAGAAGAATCACAGCCCTCCACCCCGAAACCGAA
mitchelli    TAACCCTTGTACCTTTTGCATCATCCTTTAGCAAGAATATAAGGACAAGAAGAATCACAGCCCCAACCCC-GAAACCGAA
molossus     TAACCCTTGTACCTTTCGCATCATGGTCTAGCAAGAATACAAGGACAAGAAGAATCACAGCCCACC-CCCCGAAACCGAA
muta         --------------------------------------------------------------------------------
piscivorus   CAACTCTTGTACCTTTTGCATCATGGTTTAGCAAGAACCCAGGGACAAGAAGAATCAAAGCCCCTCCCCCCGAAACCGAA
polystictus  TAACCCTTGTACCTTTTGCATCATGGTTTAGCAAGAATACAAGGACAAGAAGAATCATAGCCTACC-CCCCGAAACCGGA
pricei       TAACCCTTGTACCTTTCGCATCATGATTTAGCAAGAACATAAGGACAAGATGAATCACAGCCCTTAACCCCGAAACCGAA
pusillus     GAAACCTTGTACCTTTTGCATCATGGTTTAGCAAGAATA-TAGGACAAGAAGAATCACAGCCCACCCCCCCCGAAACCGAA
ravus        TAACCCTTGTACCTTTTGCATCATGGTCTAGCAAGAATATAAGGGCAAGAAGAACCACAGCCCACCCCCC-GAAACCGAA
ruber        TAACCCTTGTACCTTTTGCATCATGGTTTAGCAAGAACATAAGGACAAGAAGAATCACAGCCCCCCCCCCCCGAAACCGAA
scutulatus   TTATCCTCGTACCTTTTGCATCATGGTTTAGCAAGAATATAAGGACAAGAAGAATCATAGCCCCCCACCCCCGAAACCGAA
stejnegeri   --------------------------------------------------------------------------------
tigris       TAACCCTTGTACCTTTTGCATCATGGTTTAGCAAGAATACAGGG-CAAGAAGAATCACAGCCCCAC-CCCCGAAACCGAA
tortugensis  TAACCCTTGTACCTTTTGCATCATGGTTTAGCAAGAACAAAAGGACAAGAAGAATCACAGCCCCCACCCCCCGAAACCGAA
transversus  --------------------------------------------------------------------------------
triseriatus  TAACCCTTGTACCTTTTGCATCATGGTTTAGCA--AATCACAGGACAAGAAGAATCACAGCCCACCCCCCCCGAAACCGAA
unicolor     TAACCCTTGTACCTTTTGCATCATGGTCTAGCAAGTATATAAGGACAAGAAGAATCATAGCCCCCCTCCCCGAAACCGAA
vegrandis    TAACCCTTGTACCTTTTGCATCATGGTCTAGCAAGAATATAAGGACAAGAAGAATCATAGCCCCAC-CCCCGAAACCGAA
viridis      TAACCCTTGTACCTTTTGCATCATGGTTTAGCAAGGATATAAGGACAAGAAGAATCACAGCCCCCCACCCCGAAACCGAA
willardi     TAGCCCTTGTACCTTTTGCATCATGGTCTAGCAAGAATACAAGGACAAGAAGAATCATAGCCCCACCCCCCCGAAACCGAA
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             801      810        820        830        840        850        860        870        880
adamanteus   CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
aquilus      CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
atrox        CGAGCTATTTTCAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAAGAGTGGGAAGACTTAAAAATACAGGTGAAAC
basiliscus   CGAGCTATTTTTAAGCAGTCTAACGGACAAACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
bilineatus   --------------------------------------------------------------------------------
blomhoffii   ????????????????????????????????????????????????????????????????????????????????
catalinensisCGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
catenatus    CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTGAAAATAGAGGTGAAAC
cerastes     CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
contortrix   TGAGCTATTTTTAAGCAGTCTAACGGACAAACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
durissus     CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
enyo         CGAGCTATTTTCAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
horridus     CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCCATGTAGCAAAATGGTGGGAAGACTTAAAAATAGAGGTGAAAC
intermedius CGAGCTATTTTTAAGCAGTCTAACGGACTCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
lepidus      CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
miliarius    CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTGGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
mitchelli    CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
molossus     CGAGCTATTTTTAAGCAGTCTAACGGACGAACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
muta         --------------------------------------------------------------------------------
piscivorus   TGAGCTATTTTTAAGCAGTCTAACGGACGAACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
polystictus  CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
pricei       CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTGAAAATAGAGGTGAAAC
pusillus     CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTTGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
ravus        CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
ruber        CGAGCTATTTTCAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
scutulatus   CGAGCTATTTTTGAGCAGTCTAATGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
stejnegeri   --------------------------------------------------------------------------------
tigris       CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
tortugensis  CGAGCTATTTTCAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
transversus  --------------------------------------------------------------------------------
triseriatus  CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGAAAGACTTAAAAATAGAGGTGAAAC
unicolor     CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
vegrandis    CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
viridis      CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
willardi     CGAGCTATTTTTAAGCAGTCTAACGGACGCACCCTTCTATGTAGCAAAATAGTGGGAAGACTTAAAAATAGAGGTGAAAC
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             881     890       900       910       920       930       940       950       960
adamanteus   GCCTACCGAGTCCGGAGATAGCTGGCTACCCC-AAACAGAATCTTAGTTCTACTTTAGAA-CAACACTTAATCAATT-AA
aquilus      GCCTACCGAGTCCGGAGATAGCTGGCTACCCC-AAATAGAATCTAAGTTCTACTTTAGAA-CAACACTTAATCAATT-AA
atrox        GCCTACCGAGTTCGGAGATAGCTGGCTACCCC-AAACAGAATCTAAGTTCTACTTTAGATACAACACTTAATCTATT-AA
basiliscus   GCCTACCGAGTCCGGAGATAGCTGGCTACCCC-AAACAGAATCTAAGTTCTACTTTAGAAACAACACTTAATCAATT-AA
bilineatus   ----------------------------------------------------------------------------
blomhoffii   ????????????????????????????????????????????????????????????????????????????
catalinensisGCCTACCGAGTCCGGAGATAGCTGGCTACCCC-AAACAGAATCTAAGTTCTACTTTAGATACAACACTTAATCAATT-AA
catenatus    GCCTATCGCGTCCGGAGATAGCTGGCTACCCC-AAACAGAATGTAAGTTCTACTTTAGAA-CAGAAATTAATCATTT-AA
cerastes     GCCTACCGAGTTCGGAGATAGCTGGCTACCCCAAAAAAGAATCTAAGTTCTACTTTAGAA-CCACATTTAATCAATT-AA
contortrix   GCCTATCGAATCCGGAGATAGCTGGCTACCCA-TAACAGAATCTAAGTTCTACTTTAGAG--AATACCCTATCAATT-AA
durissus     GCCTACCGAGTCCGGAGATAGCTGGCTACCCA-AAACAGAATCTAAGTTCTACTTTAGAA-CAACACTTAAACAATT-AA
enyo         GCCTACCGAGTCCGGAGATAGCTGGCTACCCAAAAAAAGAATCTAAGTTCTACTTTAGAGCCA-CACTTAATTAATT-AA
horridus     GCCTACCGAGTCCGGAGATAGCTGGCTACCCA-AAACAGAATCTAAGTTCTACTTTAGAACCGACACTTAATCAATTTAA
intermedius GCCTACCGAGTCCGGAGATAGCTGGCTACCCCACAACAGAATCTAAGTTCTACTTTAGTA-TAGCACTTAACTAATT-AA
lepidus      GCCTACCGAGCCCGGAGATAGCTGGCTACCCC-AAATAGAATCTAAGTTCTACTTTAGAA-CGGCACTTAATCAATT-AA
miliarius    GCCTATCGAGTCCGGAGATAGCTGGCTACCCC-AAACAGAATCTAAGTTCTACTTTAGAA-CAACATTTAACC-ATT-AA
mitchelli    GCCTACCGAGTCCGGAGATAGCTGGCTACCCC-AAATAGAATCTAAGTTCTACTTTAGAA-CAACACTTAATTAATC-AA
molossus     GCCTACCGAGTCCGGAGATAGCTGGCTACCCC-AAACAGAATCTAAGTTCTACTTTAGAACTAACACCTAATCAACT-AA
muta         ----------------------------------------------------------------------------
piscivorus   GCCTATCGAATCCGGAGATAGCTGGCTACCCCATAACAGAATATAAGTTCTACTTTAGAG-CAACACTTAATTAATT-AA
polystictus GCCTACCGAGTCCGGAGATAGCTGGCTACCCC-AAAAAGAATCTAAGTTCTACTTTAGAA-AAACACTTAATCAATT-AA
pricei       GCCTACCGAGTCCGGAGATAGCTGGCTACCCCACAACAGAATCTAAGTTCTACTTTAGAA-TAGCACTTAATCAATT-AA
pusillus     GCCTACCGAGTTCGGAGATAGCTGGCTACCCC-AAATGGAATCTAAGTTCCACTTTAGAA-CGACACTTAACCAATT-AA
ravus        GCCTACCGAGTCCGGAGATAGCTGGCTACCCC-AAACAGAATCTAAGTTCTACTTTAGAA-TAGCACTTAATCAATT-AA
ruber        GCCTATCGAGTCCGGAGATAGCTGGCTACCCA-AAACAGAATCTAAGTTCTACTTTAGATACAACACTTAATCAATT-AA
scutulatus   GCCTACCGAGTCCGGAGATAGCTGGCTACCCC-AAACAGAATCTAAGTTCTACTTTAGAA-CAGCGCTTAATCAATT-AA
stejnegeri   ----------------------------------------------------------------------------
tigris       GCCTACCGAGTCCGGAGATAGCTGGCTACCCC-AAACAGAATCTAAGTTCTACTTTAGAA-TAGCACTTAATCAATT-AA
tortugensis  GCCTACCGAGTCCGGAGATAGCTGGCTACCCC-AAACAGAATCTAAGTTCTACTTTAGATACAACACTTAATCAATT-AA
transversus  ----------------------------------------------------------------------------
triseriatus  GCCTACCGAGTCCGGAGATAGCTGGCTACCCC-AAATAGAATCTAAGTTCTACTTTAGAA-CAACACTTAACCAATT-AA
unicolor     GCCTACCGAGTCCGGAGATAGCTGGCTACCCA-AAACAGAATCTAAGTTCTACTTTAGAG-CAACACTTAAACTATT-AA
vegrandis    GCCTACCGAGTCCGGAGATAGCTGGCTACCCA-AAACAGAATCTAAGTTCTACTTTAGAA-CAACACTTAAACAATT-AA
viridis      GCCTACCGAGTTCGGAGATAGCTGGCTACCCC-AAACAGAATCTAAGTTCTACTTTAGAG-CAGCGCTTAATCAATT-AA
willardi     GCCTACCGAGTCCGGAGATAGCTGGCTACCCC-AAACAGAATCTAAGTTCTACTTTAGAA-CGACACTTAATCAATT-AA
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             961     970       980       990      1000      1010      1020     1030       1040
adamanteus   T-CATCTAAAGGCAGTCAATAGAGGTACAGCTCTATTGACCCAGGATACAACCTGAATTTGCAAGAAA-CTTACC-ACCA
aquilus      C-CATCTAAAGATAGTCAACAGAGGTACAGCTCTATTGACCCAGGATACAACCTGAATTTGCAAGAAAACCGACCTTTAA
atrox        T-CATCTAAAGACAGTCAACAGGGGTACAGCTCTGTTGACCCAGGATACAACCTGAATTTGCAAGAAAACCAACC-ACTA
basiliscus   T-CATCTAAAGATAGTCAACAGAGGTACAGCTCTATTGACCCAGGATACAACCTGAATTTGTAAGGAA-CCAACCT-CTA
bilineatus   ----------------------------------------------------------------------------
blomhoffii   ????????????????????????????????????????????????????????????????????????????
catalinensisT-CGTCTAAAGACAGTCAACAGGGGTACAGCTCTGTTGACCCAGGATACAACCTGAATTTGCAAGAAAACCAACC-GCCA
catenatus    T-CATCTAAAGATAGTCAGCAGGGGTACAGCTCTGTTGACCCAGGATACAACCTGAATTTGCAAGAAAA-TAACCTTTAA
cerastes     T-CATCTAAAGAAAGTCAACAGGGGTACAGCTCTGTTGATCCAGGATACAACCTGAATTTGCAAGAAA-CCAACC-TTAC
contortrix   T-CATGTAAAGACAGTCAACAGAGGTACAGCTCTGTTGACCCAGGATACAACCTGAATTTGCAAGAAA-CTGACCCACCC
durissus     C-CATCTAAAGACAGTCAACAGGGGTACAGATATGTTGACCCAGGATACAACCTGAATTTGCAAGAAA-TCAACCT-CTA
enyo         C-CATCTAAAGATAGTCAACAGGGGTACAGATATGTTGACCCAGGATACAACCTGAATTTGCAAGAAA-CCTCTTCTACC
horridus     C-CATCTAAAGGCAGTCAACAGAGGTACAGCTCTATTGACCCAGGATACAACCTGAATTTGCAAGAAA-CTAACCTTT-A
intermedius G-CATCTAAAGATAGTCAATAGGGGTACAGCTCTATTGACCCAGGATACAACCTGAATTTGCAAGAAAA-TACCTACC-A
lepidus      C-CATCTAAAGATAGTCAACAGAGGTACAGCTCTGTTGACCCAGGATACAACCTGAATTTGCAAGAAA-CTGACCTCTGC
miliarius    A-CATCTAAAGATAGTCAACAGGGGTACAGCTCTGTTGACCCAGGATACAACCTGAATTTGCAAGAAA-CTAACCTTTAA
mitchelli    C-CATCTAAAGACAGTCAACAGGGGTACAGCTCTGTTGACCCAGGATACAACCTGAATTTGTAAGAAA-CTTAACCACTA
molossus     T-AATCTAAAGGCAGTCAACAGAGGTACAGCTCTATTGACCCAGGATACAACCTGAATTTGTAAGAAA-CCAACCCCC-A
muta         ----------------------------------------------------------------------------
piscivorus   C-CATCTAAAGACAGTCAACAGGGGTACAGCTCTGTTGACCCAGGATACAACCTGAATTTGCAAGAAA-CTGATCCACCC
polystictus --CATCTAAAGACAGTCAACAGGGGTACAGCTCTGTTGACCCAGGATACAACCTGAATTTGCAAGAAA-CCAACCATT-A
pricei       T-CATCTAAAGATAGTCAATAGGGGTACAGCTCTATTGACCCAGGATACAACCTGAATTTGCAAGGAAACCCCATTTC-A
pusillus     T-CATCTAAAGACAGTCAACAGAGGTACAGCTCTGTTGACCCAGGATACAACCTGAATTTGCAAGGAAACCGACCTCT-A
ravus        T-CATCTAAAGACAGTCAACAGAGGTACAGCTCTGTTGACCCAGGATACAACCTGAATTTGCAAGAAA-CCAACTTTTAC
ruber        TTCATCTAAAGGCAGTCAACAGGGGTACAGCTCTGTTGACCCAGGATACAACCTGAATTTGCAAGAAA-CCATAATACTA
scutulatus   C-CATCTAAAGATAGTCAACAGAGGTACAGCTCTATTGACCCAGGATACAACCTGAATTTGCAAGAAA-CTAACCAACCG
stejnegeri   ----------------------------------------------------------------------------
tigris       C-CATCTAAAGGCAGTCAACAGAGGTACAGCTCTCTTGACCCAGGATACAACCTGAATTTGAAAGAAA-CTAACC-ACTA
tortugensis  T-CATCTAAAGACAGTCAACAGGGGTACAGCTCTGTTGACCCAGGATACAACCTGAATTTGCAAGAAAACCAACC-ACTA
transversus  ----------------------------------------------------------------------------
triseriatus  C-CATCTAAAGATAGTCAATAGAGGTACAGCTCTATTGACCCAGGATACAACCTGAATTTGCAAGAAA-CCAACCTTT-A
unicolor     T-CATCTAAAGACAGTCAACAGGGGTACAGATATGTTGACCCAGGATACAACCTGAATTTGCAAGAAA-TCAACCT-CTG
vegrandis    C-CATCTAAAGACAGTCAACAGGGGTACAGCTCTGTTGACCCAGGATACAACCTGAATTTGCAAGAAA-TCAACCT-CTA
viridis      C-CGTCTAAAGGAAGTCAACAGAGGTACAGCTCTGTTGACCCAGGATACAACCTGAATTTGCAAGAAA-CTAACT-ATTA
willardi     C-CGTCTAAAGACAGTCAATAGGGGTACAGCTCTATTGATACAGGATACAACCTGAATTTGCAAGGAAACCAACCACT-A
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             1041   1050      1060      1070      1080      1090      1100      1110      1120
adamanteus   CCC--A-CCCGTAGGCCCTCAAGCAGCCACCCAAAAAAATATCGTCAAAGAATT-AACCT-AAA-CTAAACCCAACACCC
aquilus      CT---ACCCCGTAGGCCCTCAAGCAGCCACCCTAAAAAATATCGTCAAAGAATT-AACTT-AAAA--AATCCAAACACCA
atrox        CCC--A-CCCGTAGGCCCTCAAGCAGCCACCATAAAAAATATCGTCAAAGAATTTAACCT-AAA-CTAAACCCAACACCC
basiliscus   TTC-TA-CCCGTAGGCCCTCAAGCAGCCACCCTAAAAAATATCGTCAAAGAATT-AACTT-AAA--TAAACCCAACACCA
bilineatus   ------------------------------------------------------------------------------
blomhoffii   ??????????????????????????????????????????????????????????????????????????????
catalinensisCC--TA-CCCGTAGGCCCTCAAGCAGCCACCATAAAAAATATCGTCAAAGAATTCAACCT-AAA-CTAAACCCAACACCC
catenatus    TC---A-CCCGTAGGCCCTCAAGCAGCCACCCTAAAAAATATCGTCAAAGAATT-AACC--AAAAC-AAACCTAATACCA
cerastes     CCTTTTTCCCGTAGGCCCTCAAGCAGCCACCCTTAAAAATATCGTCAAAGAATT-AACTT-AAA--TAAACCCTACACTA
contortrix   TTA--A-CCCGTAGGCCCTCAAGCAGCCACCCTAAAAAATATCGTCAAAGAATT-AACTT-AAAA--AATCCTAACACCA
durissus     CTTC-A-CCCGTAGGCCCTCAAGCAGCCACCCTAAAAAATATCGTCAAAGAATTTA-CCT-AAA-CTAAACCCAACACCA
enyo         ----TGCCCCGTAGGCCCTCAAGCAGCCACCCCAAAAAATATCGTCAAAGAATT-AACCT-AAAA--AACCCCAACAACA
horridus     ACC--A-CCCGTAGGCCCTCAAGCAGCCACCCTAAAAAATATCGTCAAAGAATT-AACTT-AAA-C-AAACCCAACACTA
intermedius  CTTT-A-CCCGTAGGCCCTCAAGCAGCCACCCCCAAAAATATCGTCAAAGAATT-AACCT-AAA-C-AATCCCAGCACTA
lepidus      CC---ACCCCGTAGGCCCTGAAGCAGCCACCCTAAAAAATATCGTCAAAGAATT-AACTT-AAAA--AACCCCAGCACTA
miliarius    CT---A-CCCGTAGGCCCTCAAGCAGCCACCCTAAAAAATATCGTGAAAGAATT-AACT--AAAACTAAACCCGAAACCA
mitchelli    CCT--A-CCCGTAGGCCCTCAAGCAGCCACCCAAAAAAATATCGTCAAAGAATT-AACC--AAAACTAAACCCAACACCA
molossus     TCC-TA-CCCGTAGGCCCTCAAGCAGCCACCCTAAAAAATATCGTCAAAGAATT-GACTT-AAA-C-AAACCCAACACCA
muta         ------------------------------------------------------------------------------
piscivorus   TTA--A-CCCGTAGGCCCTCAAGCAGCCACCCCAAAAAATATCGTCAAAGAATT-GACCT-AAAA-TAACCCCAACACTA
polystictus  CTT---CCCCGTAGGCCCTCAAGCAGCCACCCTAAAAAATATCGTCAAAGAATT-AACCT-AAA--TAAACCCAACACCA
pricei       CCC--A-CCCGTAGGCCCTCAAGCAGCCACCCTAAAAAATATCGTCAAAGAATT-AACTT-AAA-C-AATTCCAACACCA
pusillus     TCT--A-CCCGTAGGCCCTCAAGCAGCCACCCTAAAAAATATCGTCAAAGAATT-AACCTTAAA---AACCCCAACACCA
ravus        CTT--TCCCCGTAGGCCCTCAAGCAGCCACCCTAAAAAATATCGTCAAAGAATT-AACCT-AAAA--AATCCCAACACCG
ruber        CC--TA-CCTGTAGGCCCTCAAGCAGCCACCATAAAAAATATCGTCAAACAATTTATCCT-AAA-CTAAACCCAACATCC
scutulatus   CCT--A-CCCGTAGGCCCTCAAGCAGCCACCCAAAAAAATATCGTCAAAGAATT-AACCT-AA--CTAAATCCAACAACA
stejnegeri   ------------------------------------------------------------------------------
tigris       CCT--A-CCCGTAGGCCCTCAAGCAGCCACCCAAAAAAATATCGTCAAAGAATT-AACC--AAAACTAAACCCAACACCA
tortugensis  CCC--A-CCCGTAGGCCCTCAAGCAGCCACCATAAAAAATATCGTCAAAGAATTTAACCT-AAA-CTAAACCCAACACCC
transversus  ------------------------------------------------------------------------------
triseriatus  CC--TATCCCGTAGGCCCTCAAGCAGCCACCCTAAAAAATATCGTCAAAGAATT-AGCTT-AAAA--AACCCCAACACTA
unicolor     CTTC-A-CCCGTAGGCCCTCAAGCAGCCACCCTAAAAAATATCGTCAAAGAATTTA-CCT-AAA-CTAAACCCAACACCA
vegrandis    CTTC-A-CCCGTAG-CCCTCAAGCAGCCACCCTAAAAAATATCGTCAAAGAATTTA-CCT-AAA-CTAAACCCAACACCA
viridis      CCC--A-CCCGTAGGCCCTCAAGCAGCCACCCAAAAAAATATCGTCAAAGAATT-AACCTTAA--CTAAACCCAACACCA
willardi     CCT--A-CCCGTAGGCCCTAAAGCAGCCACCCTAAAAAATATCGTCAAAGAATT-AACTTTAAA-C-AAACCCAACACTA
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            1121   1130      1140      1150      1160      1170      1180      1900      1200
adamanteus  ACTAAGAACTTCAAATTAACTAAAGGTGAATCTACACAAGTAGATATCATTATGCTAAAACTAATAATAAGA--CCCCCC
aquilus     ACTAAAAACTTCAAACCAACTAAAGGTGAATCTACAAAAGTAGATGCCATTATGCTAAAACTAATAATAAGA-CCCCCCC
atrox       ACTAAGAACTTCAAATTAACTAAAGGTGAATCTACACAAGTAGATATCATTATGCTAAAACTAATAATAACA--CCTCCC
basiliscus  ACTAAAAACTTCAAATTAACTAAAGGTGAATCTACACCAGTAGATAACACTATGCTAAAACTAATAATAAGA-CC---AC
bilineatus  ----------------------------------------------------------------------------
blomhoffii  ????????????????????????????????????????????????????????????????????????????
catalinensisACTAAGAACTTCAAATTAACTAAAGGTTAATCTACACAAGTAGATATCATTATGCTAAAACTAATAATAAGA-CCCCCCC
catenatus   ACCAGAAACTTCAAATTAACTAAAG-TGAATCTACATAAGTAGATATCATTATGCTAAAACTAATAATAAGA-CT---AC
cerastes    ACCAAGAACTTCAAATTAACTAAAGGTGAATCTACACAAGTAGATACCATTATGCTAAAACTAATAATAAGA-CTTC-CA
contortrix  ACCAAAAACTTCAAATTAACTAAAGGTGAGCCTACACAAGTAGACATCACTATGCTAAAACTAATAATAAGA-CCCC-AT
durissus    GCTAAGAACTTCAAATTAACTAAAGGTGAATCTACACAAGTAGATATCATTATGCTAAAACTAATAATAAGACC-CACAC
enyo        ACCAAGAACTTCAAATTAACTAAGGGTGAATCTACACAAGTAGATACCATTATGCTAAAACTAATAATAAGA-CTTTTCC
horridus    ACTAAGAACTTCAAATTAACTAAGGGTGAATTTACACAAGTAAATGTCATTATGCTAGAACTAATAATAAGA-CCTCTCC
intermedius ACTATGAACTTCAAATTAACTAAAGGTGAATCTACATAAGTAGATATCATTATGCTAAAACTAATAATAAGGGGACCCCC
lepidus     ACTAAAAACTTCAAATCAACTAAAGGTGAATCTACACAAGTAGATACCATTATGCTAAAACTAATAATAAGATCCCCTCC
miliarius   ATTAAAAACTTCAAACTAACTAAAGGTGAACCTACATTAGTAGATATCATTATGCTAAAACTAATAATAAGA-GGTCC-C
mitchelli   ACTAAGAACTTCAAACTAACTAAAGGTGAATCTACACAAGTAGATATCATTATGCTAAAACTAATAATAAGA-CCCC-CC
molossus    ACTAAAAACTTCAAATTAACTAAAGGTGAATCTACACCAGTATGTAACATTATGCTAAAACTAATAATAACA-CCT---C
muta        ----------------------------------------------------------------------------
piscivorus  ATTAAAAACTTCAAATTAACTAAAGGTGGGCCTACACAAGTAGACACCATTATGCTAAAACTAATAATAAGA---TCCC-
polystictus ACCAAGAACTTCAAACTAACTAAAGGTGAATCTACACGAGTAGATACCATTATGCTAAAACTAATAATAAGA-CCCAC-C
pricei      ACTAGGAACTTCAAATTAACTAAAGGTGAATCTACACAAGTAGATGTCATTATGCTAAAACTAATAATAAGG---CCCCA
pusillus    ACTAAAAACTTCAAATTAACTAAAGGTGAATCTACACAAGTAGATGCCATTATGCTAAAACTAATAATAAGA-CCTC-CC
ravus       ACTAAAAACTTCAAATTAACTAAAGGTGAATCTACAAAAGTAGATACCATTATGCTAAAACTAATAATAAGA--CATTCC
ruber       ACTAAGAACTTCAAATTAACTAAAGGTGAATCTACACAAGTAGATATCATTATGCTAAAACTAATAATAAGA-CTCCCCT
scutulatus  ACTAAGAACTTCAAATTAACTAAAGGTGGATCTACACAGGTAGATATCATTATGCTAAAACTAATAATAAGA-CCA---C
stejnegeri  ----------------------------------------------------------------------------
tigris      ACCATAAACTTCAAATTAACTAAAGGTGAATCTACACAAGTAGATAACATTATGCTAAAACTAATAATAAGA-CCCCC-C
tortugensis ACTAAGAACTTCAAATTAACTAAAGGTGAATCTACACAAGTAGATATCATTATGCTAAAACTAATAATAAGA-CCCT-CC
transversus ----------------------------------------------------------------------------
triseriatus ACTAAAATCTTCAAATCAACTAAAGGTGAATCTACACAAGTAGATACCATTATGCTAAAACTAATAATAAGA--CCACCC
unicolor    GCTAAGAACTTCAAATTAACTAAAGGTGGATCTACACAAGTAGATATCATTATGCTAAAACTAATAATAAGA-CCCACAC
vegrandis   GCTAAGAACTTCAAATTAACTAAAGGTGAATCTACACAAGTACATATCATTATGCTAAAACTAATAATAAGA-CCCACAC
viridis     ACTAAGAACTTCAAATCAACTAAAGGTGAATCTACATAGGTAGATGTCATTATGCTAAAACTAATAATAAGA-C----AC
willardi    ACTAAGAACTTCAAATTAACTAAAGGTGAATCTACACAAGTAGATAACATTATGCTAAAACTAATAATAAGAGCACCCAC
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            1201   1210      1220      1230      1240      1250      1260      1270      1280
adamanteus  CCTCTCTTTACGCACCTCT-CCGCTATAAACAGA-AAAACTACTGGCAATTAAC-AGACCACAAAAGGCAAACAATAAAC
aquilus     CCTCTCTTCACGCACCCCT-CCGCTAGAAACAGA-AAATCTACTAGCAATTAAC-AGACCACAAAAGGCAAACAATAAAC
atrox       --TCTCTTTACGCACCCCT-CCGCTAGAAACAGA-AAAACTACTGGCAATTAAC-AGACCACAAAAGGCAAATAATAAAC
basiliscus  C-TCTCTTTACGCA-CCCTCCCACCAGAAACAGA-AAAACTACTGGTAGTTAAC-AGACCACAAAAGGCAAATAATAAAC
bilineatus  --------------------------------------------------------------------------------
blomhoffii  ????????????????????????????????????????????????????????????????????????????
catalinensisCCTCTCTTTACGCACCCCT-CCGCTAGAAACAGA-AAAACTACTAGCAATTAAC-AGACCACAAAAGGCAAATAATAAAA
catenatus   CCTCTCTTTACGCA-CCCTTCCGCTAGAAATAGA-AAAACTACTAGTAATTAAC-AGACCACAAAAGGCAAACAATAAAC
cerastes    AATCTCTTTACTCCCCCCCTCCGCTAGAAATAGA-AAGACTGCTAGCAATTAAC-AGACCACAAAAGGCAAACAATAAAC
contortrix  CTCTT--TTACGCACCCCT-CCGCTAGAAACAGA-AAAACTACTAGCAATTAAC-AGACCACAAAAGGCAAACAACAAAC
durissus    CCTCTCTTTACGCACCCCT-CCGCTAGAAACAGA-AAAACTACTGGCAATTAAC-AGACCACAAAAGGCAAACAATAAAC
enyo        CCTCTCTTTACGCACCCCT-CCGCTAGAAACAGA-AAAACTACTAGCAATTAAC-AGACCACAAAAGGCAAACTATAAAC
horridus    CCTCTCTTTACGCACCCCT-CCGCTAGAAACAGA-AAAACTACTAGCAATTAAC-AGACCACAAAAGGCAAACAATTAAC
intermedius CCCCTCTTAACGCA-CCCTTCCGCTAGAAATAGA-AAAACTACTAGCAATTAAC-AGACCATAAAAGGTAAACAATAAAC
lepidus     CCTCTCTTCACGCACCCCC-CGGCTAGAA-CAGA-AAAACTACTAGCAGTTAAC-AGACCACAAAAGGAAAACAATAAAC
miliarius   TCTCTCTTTACGCACCCCT-CCGCTAGAAACAGA-AAAACTACTAGCAATTAAC-AGACCACAAAAGGCAAACAATAAAC
mitchelli   CCTCTCTTTACGCA-CCCCCCAGCTAGAAACAGA-AAAACTACTAGCAGTTAACCAGACCACAAAAGGCAAACAATAAAC
molossus    CATCTCTTTACGCACCCCT-CCGCTAGAAATAGA-AAAACTACTGGCAATTAAC-AGACCATAAAAGGCAAACAATAAAC
muta        --------------------------------------------------------------------------------
piscivorus  CATCTCTTTACGCACCCCT-CCGCTAAAAACAGA-AAAACTACTAGCAATTAAC-AGACCACAAAAGGCAAACAACAAAC
polystictus CCTCTCTTTACGCACCCCT-CCGCTAGAAATAGA-AAAACTACTAGCAATTAAC-AGACCACAAAAAGTAAATAATAAAC
pricei      CCCCTCTTTACGCA-CCCTTCCGCTAGAAATAGACAAAACTACTAGCAATTAAC-AGACCACAAAAGGCAAACAATAAAC
pusillus    C-TCTCTTTACGCACCCCT-CCGCTAGAAACAGA-AAAACTACTGGCAATTAAC-AGACCACAAAAGGCAAACAATAAAC
ravus       CCTCTCTTTACGCCTCCCT-CCGCTAGAAACAGA-AAAACTACTAGCAATTAAC-AGACCACAAAAGGCAAACAATAAAC
ruber       C---TCTTTACGCACCCCT-CCACTAGAAACAGA-AAAACTACTAGCAATTAAC-AGACCACAAAAGGCAAACAACAAAC
scutulatus  CCTCTCTTTACGCACCCCT-CCGCTAGAAACAGAAAAACACTACTAGCAATTAAC-AGACCACAAAAGGCAAACAATCAAA
stejnegeri  --------------------------------------------------------------------------------
tigris      CATCTCTCAACGCACCCCT-CCGCTAGAAACAGA-AAAACTACTAGCAATTAAC-AGACCACAAAAGGCAAACAATAAAC
tortugensis CCTCTCTTTACGCACCCCT-CCGCTAGAAACAGA-AAAACTACTGGCAATTAAC-AGACCACAAAAGGCAAATAATAAAC
transversus --------------------------------------------------------------------------------
triseriatus CCTCTCTTCACGCACCCCT-CCGCTAGAAACAGA-AAAACTACTAGCAATTAAC-AGACCACAAAAGGCAAATAATAAAT
unicolor    CCTCTCTTTACGCACCCCT-CCGCTAGAAACAGA-AAAACTACTGGCAATTAAC-AGACCACAAAAGGCAAACAATAAAC
vegrandis   CCTCTCTTTACGCACCCCT-CCGCTAGAAACAGA-AAAACTACTGGCAATTAAC-AGACCACAAAAGGCAAACAATAAAC
viridis     CCTCTCTTTACGCA-CCCTCCCGCTAGAAACAGA-AAAACTACTAGCAGTTAAC-AGACCACAAAAGGCAAACAATAAAC
willardi    CCTCTATTTACGCACCCCT-CCGCTAGAAACAGA-AAAACTACTAGCAATTAAC-AGACCACAAAAGGCAAACAATTAAC
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             1281   1290      1300      1310      1320      1330      1340      1350      1360
adamanteus   CCATGCCCATTTT-AAAACCCACTGTGACCCCGACACAGGAGCGCAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
aquilus      CAATACCCACCTT-CAAACCCACTGTGACCCCAACACAGGCGCGTAAAAAA-GAAAGATCAAACATTATAAAAGGAACTC
atrox        CCATGCCCATTTT-TAAACCTACTGTGACCCCGACACAGGCGCGCAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
basiliscus   CCATGCCCATTTT-CAAACCCACTGTGACCCCGACACAGGCGCGTAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
bilineatus   --------------------------------------------------------------------------------
blomhoffii   ????????????????????????????????????????????????????????????????????????????
catalinensisCCATACCCACTTT-TAAACCTACTGTGACCCCGACACAGGCGCGCAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
catenatus    CTATACCTACCTT-CAAACCCACTGTGACCCCAACACAGGCGCGTAAAAAA-GAAAGATTAATCATTATAAAAGGAACTC
cerastes     CTATGCCCACCTA-TAAACCCACTGTGACCCCGACACAGGTGCGTAAAAAAAGAAAGATTAACTATTATAAAAGGAACTC
contortrix   CCATACCCACCTA--AAACTAACTGTGACCCCAACACAGGCGCGTTAAAAA-GAAAGATTAACTGTTATAAAAGGAACTC
durissus     CCATGCCCATCTT-TTAACCTACTGTGACCCCAACACAGGCGCGTAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
enyo         TCATGCCCAACTA-TAAACCTACTGTGACCCCAACACAGGCGCGTAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
horridus     CCATACCCATTTT-CAAACCCACTGTGACCCCGACACAGGCGCGTAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
intermedius  CCATACACACCTT-CAAATCAACTGTAACCCCAACACAGGAGCGTAAAAAA-GAAAGATTAACCATTATAAAAGGAACTC
lepidus      CCATACCCACCTT-AAAACCCACTGTGACCCCAACACAGGCGCGTAAAAAA-GAAAGATTAACTATTATAAAAGGAAGTC
miliarius    CTATACCCACCTT-CAAACCCACTGTGACCCCAACACAGGCGCGTAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
mitchelli    CTATACCCATTTT-TAAACCCACTGTGACCCCAACACAGGCGCGTAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
molossus     CCATGCCCATTTT-CAAACCCACTGTGACCCCAACACAGGCGCGTAAAAAAAGAAAGATTAACTATTATAAAAGGAACTC
muta         --------------------------------------------------------------------------------
piscivorus   CCATGCTCACCTT-AAAACCAACTGTGACCCCAACACAGGAGCGTTAAAAA-GAAAGATTAACTGTTATAAAAGGAACTC
polystictus  CCATGCCCACCTT-AAAACCTACTGTGACCCCAACACAGGCGCGTAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
pricei       CTATATCCATCTT-CAAACCCACTGTAACCCCGACACAGGCGCGTAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
pusillus     CCATACCCACCTTCTAAACCCACTGTGACCCCAACACAGGCGCGTAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
ravus        CAATACCCACCTT-TAAACCCACTGTGACCCCAACACAGGCGCGTAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
ruber        CCATACCCACTTT-TAAACCTACTGTGACCCCGACACAGGCGCGCAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
scutulatus   CCATGCCCATTTT-CAAACCCACTGTGACCCCGACACAGGCGCGCAAAAAA-GAAAGATTGACCATTATAAAAGGAACTC
stejnegeri   --------------------------------------------------------------------------------
tigris       CCATACCCATTTT-CAAAGGTACTGTGACCCCGACACAGGCGCGCAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
tortugensis  CCATACCCACTTT-TAAACCTACTGTGACCCCGACACAGGCGCGCAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
transversus  --------------------------------------------------------------------------------
triseriatus  CCATACCCACCTT-CAAACCTACTGTGACCCCGACACAGGCGCGTAAAAAA-GAAAGATTAACCATTATAAAAGGAACTC
unicolor     CCATGCCCATCTT-TTAACCTACTGTGACCCCAACACAGGCGCGTAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
vegrandis    CCATGCCCATCTT-TTAAGGTACTGTGACCCCAACACAGGCGCGTAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
viridis      CCGTACCCATTTT-CAAACCCACTGTGACCCCGACACAGGCGCGCAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
willardi     CCATACCCATTTT-CAAACCTACTGTGACCCCGACACAGGCGCGTAAAAAA-GAAAGATTAACTATTATAAAAGGAACTC
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             1361   1370      1380      1390      1400      1410      1420      1430      1440
adamanteus   GGCAACCAAGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-CAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
aquilus      GGCAACCGAGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-TAAGCAAGTATTAAAG-CAACGCCTGCCCAGTGA
atrox        GGCAACCAAGGACTCCAACTGTTTAACAAAAACATAACCTTTAGC-CAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
basiliscus   GGCAACCGGGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-TAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
bilineatus   ------------------------------------------------------------------------------
blomhoffii   ??????????????????????????????????????????????????????????????????????????????
catalinensisGGCAACCAGGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-CAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
catenatus    GGCAACCAGGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-CAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
cerastes     GGCAACCAAGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-TAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
contortrix   GGCAACCCCGGACTCCAACTGTTTAACAAAAACATAACCTTTAGC-CAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
durissus     GGCAACCAAGGACTCCAACTGTTTAACAAAAACATAACCTTTAGC-TAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
enyo         GGCAACCAAGGACTCCAACTGTTTAACAAAAACATAACCTTTAGCCTAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
horridus     GGCAACCATGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-TAAACAAGTATTAAAGGCAA---CTGCCCAGTGA
intermedius  GGCAACCAGGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-CAAACAAATATTAAAG-CAACGCCTGCCCAGTGA
lepidus      GGCAACCAAGGACTCCAACTGTTTAACAAAAACATAACCTTTAGC-TAAGCAAGTATTAAAG-CAACGCCTGCCCAGTGA
miliarius    GGCAATCGCGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-TAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
mitchelli    GGCAACCAAGGACTCCAACTGTTTAACAAAAACATAACCTTTAGC-CAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
molossus     GGCAACCAGGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-TAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
muta         ------------------------------------------------------------------------------
piscivorus   GGCAACCCCGGACTCCAACTGTTTAACAAAAACATAACCTTTAGC-CAAACAAGTATTAAAG-CGACGCCTGCCCAGTGA
polystictus  GGCAACCAAGGACTCCAACTGTTTAACAAAAACATAACCTTTAGC-TAAACAAGTATTAAAG-CGACGCCTGCCCAGTGA
pricei       GGCAACCAAGGACTCCAACTGTTTAACAAAAACATAACCTTTAGC-CAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
pusillus     GGCAACCAAGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-TAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
ravus        GGCAACCAAGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-TAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
ruber        GGCAACCAAGGACTCCAACTGTTTAACAAAAACATAACCTTTAGC-CAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
scutulatus   GGCAACCAGGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-CAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
stejnegeri   ------------------------------------------------------------------------------
tigris       GGCAACCAAGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-CAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
tortugensis  GGCAACCAAGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-CAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
transversus  ------------------------------------------------------------------------------
triseriatus  GGCAACCAAGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-TAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
unicolor     GGCAACCAAGGACTCCAACTGTTTAACAAAAACATAACCTTTAGC-TAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
vegrandis    GGCAACCAAGGACTCCAACTGTTTAACAAAAACATAACCTTTAGC-TAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
viridis      GGCAACCGAGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGT-TAAACAAGTATTAAAG-CGACGCCTGCCCAGTGA
willardi     GGCAACCAAGGGCTCCAACTGTTTAACAAAAACATAACCTTTAGC-TAAACAAGTATTAAAG-CAACGCCTGCCCAGTGA
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             1441   1450      1460      1470      1480      1490      1500      1510      1520
adamanteus   AAAA-TTTAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
aquilus      AAAA-TTCAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
atrox        AAGA-TTCAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCCATTTGTCTATTAATTGTAGACCAGTATGAAA
basiliscus   AAAA-TTTAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCTGTATGAAA
bilineatus   ----------------------------------------------------------------------------
blomhoffii   ????????????????????????????????????????????????????????????????????????????
catalinensisAAGA-TTCAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
catenatus    AAAA-TTCAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
cerastes     AAAA-TTCAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
contortrix   AAAA-TTAAACGGCCGCGGTATCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
durissus     AGAA-TTTAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
enyo         AAAA-TTTAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
horridus     AAAA-TTCAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTATACCAGTATGAAA
intermedius  AAAA-TTTAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
lepidus      AAA--TTCAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
miliarius    AAAA-TTCAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-CTTGTCTATTAATTGTAGACCGGTATGAAA
mitchelli    AAAA-TTTAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
molossus     AAAA-TTTAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCCGTATGAAA
muta         ----------------------------------------------------------------------------
piscivorus   AAAA-TTAAACGGCCGCGGTATCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCTGTATGAAA
polystictus  AATA-TTCAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCGGTATGAAA
pricei       AAAA-TTTAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCAATTTGTCTATTAATTGTAGACCAGTATGAAA
pusillus     AAAAATTTAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
ravus        AAAA-TTTAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCAATTTGTCTATTAATTGTAGACCAGTATGAAA
ruber        AAGA-TTCAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
scutulatus   AAAA-TTCAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
stejnegeri   ----------------------------------------------------------------------------
tigris       AAAA-TTTAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
tortugensis  AAGA-TTCAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
transversus  ----------------------------------------------------------------------------
triseriatus  AAAA-TTTAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
unicolor     AAAA-TTTAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
vegrandis    AGAA-TTTAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
viridis      AAAA-TTCAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
willardi     AAAA-TTTAACGGCCGCGGTACCCTAACCGTGCAAAGGTAGCATAATCA-TTTGTCTATTAATTGTAGACCAGTATGAAA
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             1521   1530      1540      1550      1560      1570      1580      1590      1600
adamanteus   GGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATACTAACATA
aquilus      GGCAAAATGAGAGCCCAGCTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATACTAACATA
atrox        GGCAAAATGAGAGCCCGACTGTCTCTTATAATAAATCAATTAAACTGATCCCCTAGTACAAAAGCTAGAATACCAACATA
basiliscus   GGCAAAATGAGAGCCCAACTGTCTCTTATAATAGATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATATCAACATA
bilineatus   --------------------------------------------------------------------------------
blomhoffii   ????????????????????????????????????????????????????????????????????????????????
catalinensisGGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATACCAACATA
catenatus    GGCAAAATGAGAGCCCGACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATTTTAACATA
cerastes     GGCAAAATGAGAGCCCGACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATACTAACATA
contortrix   GGCAAAATGAGAGCCCAACTGTCTCTTATAACAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGTATATTATCATA
durissus     GGCAAAATGAGAGCCCAACTGTCTCTTATAATAGATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATATCAACATA
enyo         GGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATACCAACATA
horridus     GGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGTATACTAACATA
intermedius  GGCAAAATGAGAGCCCAACTGTCTCCTATAATAAATCAATTAAACTGATCTTCTAGTACAAAAGCTAGGATACTAACATA
lepidus      GGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATACTAACATA
miliarius    GGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTTCTAGTACAAAAGCTAGGATACTAACATA
mitchelli    GGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATACTAACATA
molossus     GGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATACCAACATA
muta         --------------------------------------------------------------------------------
piscivorus   GGCAAAATGAGAGTCCAACTGTCTCTTATAACAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATATTAACATA
polystictus  GGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATGTCAACATA
pricei       GGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTTCTAGTACAAAAGCTAGTATACCCACATA
pusillus     GGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATACTATCATA
ravus        GGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATACTAACATA
ruber        GGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATACCAGCATA
scutulatus   GGCAAAATGAGAGCCCAGCTGTCTCTTATAGTAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATACTAACAGA
stejnegeri   --------------------------------------------------------------------------------
tigris       GGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATACTAACATA
tortugensis  GGCAAAATGAGAGCCCGACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATACCAACATA
transversus  --------------------------------------------------------------------------------
triseriatus  GGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATACTAACATA
unicolor     GGCAAAATGAGAGCCCAACTGTCTCTTATAATAGATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATATCAACATA
vegrandis    GGCAAAATGAGAGCCCAACTGTCTCTTATAATAGATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATATCAACATA
viridis      GGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATACTAACATA
willardi     GGCAAAATGAGAGCCCAACTGTCTCTTATAATAAATCAATTAAACTGATCTCCTAGTACAAAAGCTAGAATAATAACATA
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             1601   1610      1620      1630      1640      1650      1660      1670      1680
adamanteus   AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAACCTAGTAATAACTACTTTCGGTTGGGGCGACCTTGGAATA
aquilus      AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAACCCAATAATAACTACTTTTGGTTGGGGCGACCTTGGAATA
atrox        AGACCAGAAGACCCTGTGAAGCTTTAACGAACCTATTAAACCCAATAATAACTAGTTTCGGTTGGGGCGACCTTGGAACA
basiliscus   AGACCAGAAGACCCTGTGAAGCTTCAACTAACCTATTAAACCCAATAATAACTACTTTCGGTTGGGGCGACCTTGGAATA
bilineatus   ------------------------------------------------------------------------------
blomhoffii   ??????????????????????????????????????????????????????????????????????????????
catalinensisAGACCAGAAGACCCTGTGAAGCTTTAACAAACCTATTAAACCTAATAATAACTACTTTCGGTTGGGGCGACCTTGGAATA
catenatus    AGACCAGAAGACCCTGTGAAGCTTTAATTAAACTATTAAACCTTATAATAACTACTTTCGGTTGGGGCGACCTTGGAACA
cerastes     AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAACCCAATAATAACTACTTTCGGTTGGGGCGACCTTGGAATT
contortrix   AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAACCCTACTAATAACTACTTTCGGTTGGGGCGACCTTGGAATA
durissus     AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAACCAAATAATAACTACTTTCGGTTGGGGCGACCTTGGAATA
enyo         AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAACCCAATAATAATTACTTTCGGTTGGGGCGACCTTGGAACA
horridus     AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAACCTAATAATAGCTACTTTTGGTTGGGGCGACCTTGGAATA
intermedius AGACCAGAAGACCCTGTGAAGCTTTAATTAAACTATTAAAACCCATAATAATTACTTTCGGTTGGGGCGACCTCGGAATA
lepidus      AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAACCCAATAATAATTACTTTTGGTTGGGGCGACCTTGGAATA
miliarius    AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAATCCTAATAATAACTACTTTCGGTTGGGGCGACCTTGGAACA
mitchelli    AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAACCCAATAATAATTACTTTCGGTTGGGGCGACCTTGGAACA
molossus     AGACCAGAAGACCCTGTGAAGCTTTAACTAGCCTATTAAACCCAATAATAATTACTTTCGGTTGGGGCGACCTTGGAATA
muta         ------------------------------------------------------------------------------
piscivorus   AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAACCAAGTAATAGCTACTTTCGGTTGGGGCGACCTTGGAATA
polystictus AGACCAGAAGACCCTGTGAAGCTTTAACTAAACTATTAAACCCAATAATAACTACTTTTGGTTGGGGCGACCTTGGATTA
pricei       AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAACCACATAATAACTACTTTCGGTTGGGGCGACCTTGGAATA
pusillus     AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAACCCAATAATAGTTACTTTTGGTTGGGGCGACCTTGGAATA
ravus        AGACCAGAAGACCCTGTGAAGCTTTAACTAAACTATTAAACCTAATAATAACTACTTTCGGTTGGGGCGACCTTGGAATA
ruber        AGACCAGAAGACCCTGTGAAGCTTTAACGAACCTATTAAATCCAATAATAACTACTTTTGGTTGGGGCGACCTTGGAATA
scutulatus   AGACCAGAAGACCCTGTGAAGCTTTAACTAAACTATTAAACCCAATAATAACTACTTTCGGTTGGGGCGACCTTGGAAGA
stejnegeri   ------------------------------------------------------------------------------
tigris       AGACCAGAAGACCCTGTGAAGCTTTAATTAAACTATTAAACCTAATAATAATTACTTTAGGTTGGGGCGACCTTGGAATA
tortugensis  AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAACCCAATAATAACTACTTTCGGTTGGGGCGACCTTGGAACA
transversus  ------------------------------------------------------------------------------
triseriatus  AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAACCCAATAATAATTACTTTTGGTTGGGGCGACCTTGGAATA
unicolor     AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAACCAAATAATAACTACTTTCGGTTGGGGCGACCTTGGAATA
vegrandis    AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAACCAAATAATAACTACTTTCGGTTGGGGCGACCTTGGAATA
viridis      AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAGCCTAATAATAGCTACTTTCGGTTGGGGCGACCTTGGAATA
willardi     AGACCAGAAGACCCTGTGAAGCTTTAACTAACCTATTAAACCCAATAATAGCTATTTTCGGTTGGGGCGACCTTGGAATA
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             1681   1690      1700      1710      1720      1730      1740      1750      1760
adamanteus   AAAAAGAACTTCCAACATATGAATT-CTCATAAAATTAGGCAAACAA-GCCAACACC-AGACCCAGCACAGCTGACAATT
aquilus      AAAAAGAACTTCCAACATATGACTTCCTCATAAAATCAGGCAAACAA-GCCAAAACT-AGACCCAGCACAGCTGATAATT
atrox        AAAAAGAACTTCCAACACATGACTT-CTCATAAAAT-AGGCAAACAA-GCCAACACC-AGACCCAGCACAGCTGATAATT
basiliscus   AAAAAGAACTTCCAATATATGACTTCCTCATAAAAC-AGGCAGACAG-GCCATCAT--AGACCCAGCACAGCTGATAATT
bilineatus   --------------------------------------------------------------------------------
blomhoffii   ????????????????????????????????????????????????????????????????????????????
catalinensisAAAAAGAACTTCCAACACATGACTTCCTCATAAAAT-AGGCAAACAA-GCCAACACC-AGACCCAGCACAGCTGATAATT
catenatus    AAAAAGAACTTCCAACATATGACTTCCTCATTAAAC-AGGCAAACAA-GCCTATACA-AGACCCAGCACAGCTGATAATT
cerastes     AAAAAGAACTTCCAACATATGACTTCCTCATAAAAC-AGGCTAACAA-GCCAACAAT-AGACCCAGCACAGCTGATAAAT
contortrix   AAAAAGAACTTCCAATATATGACTTCCT-ATAAA-CAAGGCAAACAA-GCCAATATT-AGACCCAGCATAGCTGATAATT
durissus     AAAAAGAACTTCCAATATATGACTTCCTCATAAAAC-AGGCAAACAA-GCCAATACC-AGACCCAGCACAGCTGATAATT
enyo         AAAAAGAACTTCCAACACATGACTTACTCATAAAAT-AGGCAAACAA-GCCAACACC-AGACCCAGCACAGCTGATAATT
horridus     AAAAAGAACTTCCAATTCATGACCTCCTCATAAAATCAGGCAAACAA-GCCAACACC-AGACCCAGCACAGCTGATAATT
intermedius  AAAAAGAACTTCCAACACATGACTATCTCATAAAAC-AGGCAAACAA-GCCAACACC-AGACCCAGCACAGCTGATAATT
lepidus      AAAAAGAACTTCCAACATATGACTTCCTCATAAAAC-AGGCAAACAA-GCCAAAACT-AGACCCAGCACAGCTGATAATT
miliarius    AAAAAGAACTTCCAATACATGACTT-CTCATTAAAC-AGGCAAACAG-GCCAATAAA-AGACCCAGCACAGCTGATAATT
mitchelli    AAAAAGAACTTCCAACATATGACTTA-TCATAAAACTAGGCAAACAG-GCCAACACC-AGACCCAGCACAGCTGACAATT
molossus     AAAAAGAACTTCCAATATATGACTTCCTCATAAAAC-AGGCAAACAA-GCCAATACCTAGACCCAGCACAGCTGATAATT
muta         --------------------------------------------------------------------------------
piscivorus   AAAAAGAACTTCCAATATATGACTTCCTCATAAATCAAGGCAAACAA-GCCAATATT-AGACCCAGTATAGCTGATAATC
polystictus  AAAAAGACCTTCCAACATGTGACTT-CTCACAAAAT-AGGCAAACA--GCCAACACC-AGACCCAGCACAGCTGATAACT
pricei       AAAAAGAACTTCCAACATATGACACCCTCATAAAAT-AGGCAAACAA-GCCAACACC-AGACCCAGCAGAGCTGATAATT
pusillus     AAAAAGAACTTCCAACATATGACTCCCTCATAAAAC-AGGCAAACAA-GCCAACACT-AGACCCAGCACAGCTGATAATT
ravus        AAAAAGAACTTCCAACACATGACTTCCTCATTAAAC-AGGCAAACAG-GCCAACACT-AGACCCAGCATAGCTGATAATT
ruber        AAAAAGAACTTCCAATACATGACTT-CTCATAAAAT-AGGCAAACAA-GCCAACACC-AGACCCAGCACAGCTGATAATT
scutulatus   AAAAAGAACTTCCAATATATGACTTAC-CATAAAAT-AGGCAAACAA-GCCAACACC-AGACCCAGCACAGCTGATAATT
stejnegeri   --------------------------------------------------------------------------------
tigris       AAAAAGAACTTCCAATATATGACTTACTCATAAAAT-AGGCAGACAC-GCCAACACC-AGACCCAGCATAGCTGATAATT
tortugensis  AAAAAGAACTTCCAACACATGACTT-CTCATAAAAT-AGGCAAACAA-GCCAACACC-AGACCCAGCACAGCTGATAATT
transversus  --------------------------------------------------------------------------------
triseriatus  AAAAAGAACTTCCAACATATGACTTCCTCATAAAAC-AGGCAAACAG-GCCAACATT-AGACCCAGCACAGCTGATAATT
unicolor     AAAAAGAACTTCCAATATATGACTTCCTCATAAAAC-AGGCAAACAA-GCCAATACC-AGACCCAGCACAGCTGATAATT
vegrandis    AAAAAGAACTTCCAATATATGACTTCCTCATAAAAC-AGGCAAACAA-GCCAATACC-AGACCCAGCACAGCTGATAATT
viridis      AAAAAGAACTTCCAATACATGACTTA-TCATAAAAT-AGGCAAACAA-GCCAACACC-AGACCCAGCACAGCTGATAATT
willardi     AAAAAGAACTTCCAATATATGACTTACTCATAAAAC-AGGCAAACAA-GCCGACACT-AGACCCAGCACAGCTGATAATT
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             1761   1770      1780      1790      1800      1810      1820      1830      1840
adamanteus   GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
aquilus      GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
atrox        GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGCCCTCGATGTTG
basiliscus   GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
bilineatus   ------------------------------------------------------------------------------
blomhoffii   ??????????????????????????????????????????????????????????????????????????????
catalinensisGAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
catenatus    GAAATAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGTCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
cerastes     GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGTCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
contortrix   GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTTAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
durissus     GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACAACCTCGATGTTG
enyo         GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
horridus     GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
intermedius GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
lepidus      GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTTGATGTTG
miliarius    GAAATAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
mitchelli    GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
molossus     GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
muta         ------------------------------------------------------------------------------
piscivorus   GAAATAAGTTACTCCAGGGATAACAGCGCTATCTTCTTTAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATCTTC
polystictus GAAATAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
pricei       GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGTCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
pusillus     GAAATAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
ravus        GAAATAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
ruber        GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
scutulatus   GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
stejnegeri   ------------------------------------------------------------------------------
tigris       GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
tortugensis  GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
transversus  ------------------------------------------------------------------------------
triseriatus  GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
unicolor     GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
vegrandis    GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCT-GAGGTTG
viridis      GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
willardi     GAAACAAGTTACTCCAGGGATAACAGCGCTATCTTCTTCAAGAGCCCATATCAAAAAGAAGGTTTACGACCTCGATGTTG
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             1841   1850      1860      1870      1880      1890      1900
adamanteus   GATCAGGACATCCCCGTAATGCAGCCTTTAC--AAGGTTCGTTTGTTCAACGATTAACAGTCC--
aquilus      GATCAGGACATCCAAGTAATGCAGCCGTTACTAAAGGTTCGTTTGTTCAACGATTAACAGTCCC-
atrox        GATCAGGAACTCCAAGTAATGCAGCCGTTACTAAAGGTTCGTTTTTTCAACGATTAACAGTCCT-
basiliscus   GATCAGGACATCCAAGTAATGCAGC-GTTACTAAAGGTTCGTTTGTTCAACGATTAACAGTCCT-
bilineatus   ------------------------------------------------------------
blomhoffii   ????????????????????????????????????????????????????????????
catalinensisGATCAGGCCTCCCCAGTAATGCAGCCGTTAC--AAGGTTCGTTTGTTCAACGATTAACAGTCCT-
catenatus    GATCAGGACATCCCAGTAATGCACC-GTTACTAAAGGTTCGTTTGTTCAACGATTAACAGTCCC-
cerastes     GATCAGGACATCCA-GTAATGCAGCCGTTACTAAGGGTTCGTTTGTTCAACGATTAACAGTCCT-
contortrix   GATCAGGACATCCCAGTAATGCAACCGTTACTAAAGGTTCGTTTGTTCAACGATTAACAGTCCT-
durissus     GATCAGGACATCCAAGTAATGCAGCCGTTACTAAAGGGTCGTTTGTTCAACGATTAACAGTCCC-
enyo         GATCAGGACCCCCCAGTAATGCCCCCGTTACAAAAGGTTCGTTTGTTCAACGATTAACAGCCCT-
horridus     GATCAGGACATCCAAGTAATGCAGCCGTTACTAAAGGTTCGTTTGTTCAACGATTAACAGTCCCA
intermedius GATCAGGACATCCAAGTAATGCAGCCGTTACTGAAGGTTCGTTTGTTCAACGATTAATAGTCCT-
lepidus      GATCAGGACATTCAAGTAATGCAGCCGTTACTTAAGGTTCGTTTGTTCAACGATTAACAGTCC--
miliarius    GATCAGGACATCCCAGTAATGCAGCCGCTACTAAAGGTTCGTTTGTTCAACGATTAATAGTCCC-
mitchelli    GATCAGGACATCCAAGTAATGCAGCCGTTACTAAAGGTTCGTTTGTTCAACGATTAACAGTCCT-
molossus     GATCAGGACATCCAAGTAATGCAGCCGTTACTAAAGGTTCGTTTGTTCACCGATTAACAGTCCT-
muta         ------------------------------------------------------------
piscivorus   CATCAGGACATCCCAGTAATGCAGCCGTTACTAAAGGTTCGTTTGTTCAACGATTAACAGTCCT-
polystictus GTACAGGACATCCAAGTAATGCCGCCGTTAC-AAAGGTTCGTTTGTTCAACTATTAACAGTCCT-
pricei       GATCAGGACATCCAAGTAATGCAGCCGTTACTAAAGGTTCGTTTGTTCAACGATTAACAGTCCT-
pusillus     GATCAGGACATCCAAGTAATGCAGCCGTTACTAAAGGTTCGTTTGTTCAACGATTAACAGTCCC-
ravus        GATCAGGACATCCTAGTAATGCAGCCGTTACTAAAGGTTCGGTTGTTCAACGATTAACAGTCCC-
ruber        GATCAGGACATCCAAGTAATGCAGCCGTTACTAAAGGTTCGTTTGTTCAACGATTAACAGTCCT-
scutulatus   GATCAGGACATCCAAGTAATGCAGCCGTTACTAAAGGTTCGTTTGTTCAACGATTAACAGTCCT-
stejnegeri   ------------------------------------------------------------
tigris       GATCGGGACATCCAAGTAATGCAGCCGTTACTAAAGGTTCGTTTGTTCAACGATTAACAGTCCT-
tortugensis  GATCAGGACATCCAAGTAATGCAGCCGTTACTAAAGGTTCGTTTGTTCAACGATTAACAGTCCT-
transversus  ------------------------------------------------------------
triseriatus  GATCAGGACATCCAAGTAATGCAGCCGTTACTAAAGGTTCGTTTGTTCAACGATTAACAGTCCC-
unicolor     GATCAGGACATCCAAGTAATGCAGCCGTTACTAAAGGTTCGTTTGTTCAACGATTAACAGTCCT-
vegrandis    GATCAGGACATCCAAGTAATGCAGCCGTTACTAAAGGTTCGTTTGTTCAACGATTAACAGTCCT-
viridis      GATCAGG-CATCCAAGTAATGCAGCCGTTACTAAAGGTTCTGTTGTTCAACGATTAACAGTCCT-
willardi     GATCAGGACACCCAAGTAATGCAACCGTTACTAAAGGTTCGGTTGTTCAACGATTAATAGTCC--
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Appendix G

List of Character State Changes for Most-Parsimonious Tree

Character changes supporting internal numbered stems of the shortest tree found using the combined morphological and molecular data set, excluding 96 ambiguously aligned sites (numbered stems correspond to numbers from Figure 30). Character numbers correspond character numbers in (NEXUS) data matrix (Appendix D). Single width arrows indicate ambiguous change to derived character state and double width arrows indicate change that is unambiguous. Parsimony cost of number of unweighted steps depends on weight of that character (see Appendix D for character weights).

Branch 1
ACCTRAN: 1 (4) A-->E; 4 (3) A==>D; 5 (1) F==>G; 7 (6) A-->G; 8 (5) A-->F; 11 (5) A-->F; 12 (7) A-->H; 13 (4) A-->E; 19 (12) Y-->M; 25 (6) S-->Y; 34 (18) A-->S; 36 (2) S-->U; 43 (4) G-->K; 77 (10) A-->K; 81 (20) A-->U; 103 (8) M-->E; 109 (6) S-->Y; 110 (4) A-->E; 111 (4) A-->E; 116 (9) G-->P; 117 (4) A-->E; 119 (6) G-->A; 123 (4) Y-->U; 133 (2) I-->G; 136 (10) A-->K; 151 (4) Y-->U; 157 (19) Y-->F; 168 (12) M-->Y; 177 (3) M-->P; 180 (10) F-->P; 182 (12) A-->M; 183 (1) A-->C; 184 (24) A-->Y; 201 (4) Y-->U; 213 (6) Y==>S; 214 (6) A-->G; 219 (4) M-->Q; 227 (2) G-->I; 228 (1) B-->A; 234 (8) Q-->Y; 248 (5) A-->F; 254 (24) Y-->A; 258 (24) Y-->A; 265 (3) I-->F; 271 (2) S-->U; 283 (6) Y-->S; 284 (12) Y-->M; 285 (12) Y-->M; 287 (2) S-->U; 289 (10) A-->K; 292 (4) A-->E; 294 (6) G-->A; 296 (12) Y-->M; 303 (24) A-->Y; 340 (1) A-->G; 351 (1) A-->G; 359 (1) A-->C; 422 (1) C-->T; 447 (1) C-->T; 473 (1) C-->T; 477 (1) A-->C; 478 (1) C-->T; 494 (1) A-->C; 498 (1) C-->T; 544 (1) C-->T; 564 (1) A-->T; 566 (1) C-->T; 569 (1) C-->T; 575 (1) C-->T; 581 (1) C-->T; 649 (1) C-->T; 671 (1) A-->C; 725 (1) C-->T; 749 (1) C-->T; 798 (1) A-->T; 902 (1) C-->T; 943 (1) C-->T; 1008 (1) C-->T; 1010 (1) A-->T; 1091 (1) C-->T; 1107 (1) C-->T; 1411 (1) C-->T; 1446 (1) C-->T; 1509 (1) C-->T; 1525 (1) C-->T; 1617 (1) A-->G; 1711 (1) A-->C; 1736 (1) C-->T; 1737 (1) C-->T; 1749 (1) C-->T; 1771 (1) A-->G; 1861 (1) C-->T; 1955 (1) C-->T; 1958 (1) C-->T; 2015 (1) A-->G; 2081 (1) A-->T; 2109 (1) A-->C; 2431 (1) A-->T; 2548 (1) C-->T; 2553 (1) C-->T; 2625 (1) C-->G; 2628 (1) C-->G; 2629 (1) C-->G; 2652 (1) A-->G.
DELTRAN: 3 (10) T==>J; 4 (8) D==>L; 5 (2) G==>I; 6 (8) I==>Q; 19 (12) M-->A; 24 (16) E-->U; 34 (6) S-->Y; 41 (18) Y==>G; 43 (5) K-->P; 49 (24) A-->Y; 52 (4) Y==>U; 53 (9) Y==>P; 54 (20) Y==>E; 55 (18) S-->A; 56 (18) S-->A; 57 (12) M-->A; 64 (16) Q-->A; 66 (24) Y==>A; 80 (4) G-->K; 81 (4) U-->Y; 86 (4) Y-->U; 87 (12) M==>A; 95 (20) A-->U; 97 (10) A==>K; 99 (8) I==>A; 105 (18) Y-->G; 113 (3) M-->P; 114 (8) S-->K; 121 (5) A-->F; 124 (4) Y-->U; 125 (8) S-->K; 135 (8) A-->I; 151 (5) U-->P; 164 (24) A-->Y; 173 (12) M==>Y; 178 (3) M==>J; 179 (10) A==>K; 188 (2) S==>U; 189 (2) S==>U; 190 (3) M==>P; 191 (4) A==>E; 200 (6) S-->Y; 201 (5) U-->P; 203 (3) S==>P; 204 (6) G==>A; 208 (4) Y-->U; 212 (20) Y==>E; 213 (18) S==>A; 216 (2) I-->K; 227 (2) I-->K; 235 (15) A==>P; 245 (19) Y==>F; 253 (9) Y-->P; 261 (12) A==>M; 268 (9) S==>J; 270 (9) Y==>P; 281 (4) M==>I; 285 (2) M-->K; 292 (1) E-->F; 310 (1) A==>B; 317 (1) A-->C; 674 (1) C-->T; 803 (1) C-->T; 874 (1) A-->G; 904 (1) A-->G; 939 (1) T-->A; 1044 (1) A-->G; 1211 (1) G-->A; 1243 (1) C-->A; 1246 (1) A-->C; 1341 (1) C-->T; 1373 (1) G-->A; 1377 (1) T-->A; 1398 (1) C-->T; 1566 (1) A-->T; 1618 (1) A-->C; 1678 (1) A-->G; 1702 (1) T-->A; 1728 (1) G-->A; 1735 (1) C-->T; 1898 (1) C-->A; 1953 (1) C-->T; 2064 (1) C-->T; 2070 (1) C-->T; 2089 (1) A-->C; 2156 (1) C-->A; 2160 (1) A-->G; 2236 (1) A-->C; 2340 (1) C-->T; 2433 (1) C-->A; 2524 (1) T-->A; 2537 (1) T-->C.

Branch 2
ACCTRAN: 2 (1) E-->D; 3 (10) T==>J; 4 (8) D-->L; 5 (2) G-->I; 6 (8) I-->Q; 8 (11) F-->Q; 11 (1) F-->G; 13 (3) E-->H; 14 (2) A-->C; 19 (12) M-->A; 24 (16) E-->U; 33 (6) Y-->S; 34 (6) S-->Y; 41 (20) Y-->E; 43 (5) K-->P; 49 (24) A-->Y; 51 (4) Y-->U; 52 (4) Y-->U; 53 (9) Y-->P; 54 (20) Y-->E; 55 (18) S-->A; 56 (18) S-->A; 57 (12) M-->A; 64 (16) Q-->A; 66 (24) Y-->A; 69 (5) A-->F; 71 (8) I-->A; 76 (4) Y-->U; 77 (2) K-->M; 80 (4) G-->K; 81 (4) U-->Y; 86 (4) Y==>U; 87 (12) M-->A; 95 (24) A-->Y; 97 (10) A-->K; 99 (8) I-->A; 100 (4) A-->E; 101 (4) A-->E; 105 (18) Y-->G; 106 (5) A-->F; 110 (11) E-->P; 113 (3) M-->P; 114 (8) S-->K; 117 (6) E-->K; 121 (5) A-->F; 123 (5) U-->P; 124 (4) Y-->U; 125 (8) S-->K; 127 (2) M-->K; 135 (8) A-->I; 144 (12) Y-->M; 151 (8) U-->M; 159 (10) A-->K; 164 (24) A-->Y; 170 (6) Y-->S; 173 (12) M-->Y; 178 (3) M==>J; 179 (10) A-->K; 188 (2) S-->U; 189 (2) S-->U; 190 (3) M-->P; 191 (4) A-->E; 200 (6) S-->Y; 201 (5) U==>P; 203 (3) S-->P; 204 (6) G-->A; 208 (4) Y-->U; 212 (20) Y-->E; 213 (18) S-->A; 214 (9) G-->P; 216 (2) I-->K; 219 (2) Q-->S; 220 (5) A-->F; 224 (3) I-->F; 226 (12) Y-->M; 227 (2) I-->K; 229 (5) A-->F; 230 (14) G-->U; 235 (15) A-->P; 238 (6) S-->Y; 245 (19) Y-->F; 248 (7) F==>M; 253 (9) Y-->P; 257 (4) Y-->U; 261 (12) A-->M; 266 (4) Y-->U; 268 (9) S-->J; 269 (4) Y-->U; 270 (9) Y-->P; 277 (4) Y-->U; 281 (7) M-->F; 285 (2) M-->K; 288 (8) M-->E; 292 (1) E-->F; 293 (5) A-->F; 296 (2) M-->K; 308 (8) A-->I; 310 (1) A-->B; 803 (1) C-->T; 825 (1) T-->C; 874 (1) A-->G; 884 (1) A-->G; 904 (1) A-->G; 939 (1) T-->A; 1044 (1) A-->G; 1082 (1) A-->C; 1101 (1) C-->T; 1145 (1) G-->A; 1191 (1) T-->C; 1211 (1) G-->A; 1212 (1) T-->C; 1243 (1) C-->A; 1246 (1) A-->C; 1311 (1) C-->A; 1341 (1) C-->T; 1373 (1) G-->A; 1377 (1) T-->A; 1398 (1) C-

->T; 1419 (1) C-->A; 1432 (1) T-->A; 1508 (1) C-->T; 1513 (1) T-->C; 1550 (1) G-->A; 1566 (1) A-->T; 1589 (1) T-->C; 1618 (1) A-->C; 1678 (1) A-->G; 1702 (1) T-->A; 1728 (1) G-->A; 1735 (1) C-->T; 1887 (1) C-->T; 1898 (1) C-->A; 1938 (1) G-->A; 1953 (1) C-->T; 2064 (1) C-->T; 2070 (1) C-->T; 2089 (1) A-->C; 2114 (1) T-->A; 2133 (1) G-->A; 2156 (1) C-->A; 2160 (1) A-->G; 2236 (1) A-->C; 2250 (1) T-->C; 2340 (1) C-->T; 2433 (1) C-->A; 2503 (1) T-->A; 2524 (1) T-->A; 2537 (1) T-->C; 2587 (1) T-->C.
DELTRAN: 3 (5) J==>E; 4 (1) L-->M; 9 (1) K-->J; 10 (2) L==>J; 12 (2) H-->J; 15 (2) A-->C; 23 (2) M==>K; 24 (4) U-->Y; 39 (4) G-->K; 43 (9) P-->Y; 77 (3) M-->P; 85 (15) Y-->J; 86 (20) U==>A; 94 (10) A==>K; 104 (16) Y-->I; 113 (1) P-->Q; 144 (4) M-->I; 146 (8) Y==>Q; 178 (9) J==>A; 181 (8) M==>U; 183 (1) C-->A; 201 (10) P==>F; 210 (16) Y-->I; 214 (5) P-->U; 241 (4) G-->K; 245 (5) F-->A; 248 (8) M==>U; 257 (4) U-->Q; 279 (4) Q-->U; 285 (2) K-->I; 290 (10) A-->K; 292 (5) F-->K; 311 (1) A==>B; 814 (1) T==>C; 930 (1) A-->G; 1005 (1) T==>C; 1008 (1) T-->C; 1010 (1) T-->A; 1082 (1) A-->C; 1109 (1) T-->C; 1144 (1) A-->C; 1216 (1) A==>T; 1217 (1) C-->T; 1368 (1) T-->C; 1399 (1) A-->G; 1422 (1) C==>A; 1426 (1) C-->T; 1495 (1) T-->C; 1573 (1) T-->C; 1674 (1) T==>C; 1914 (1) A==>G; 1939 (1) C-->T; 2157 (1) C==>A; 2381 (1) T-->C; 2431 (1) T==>C; 2522 (1) T==>C; 2642 (1) C==>A.

Branch 3
ACCTRAN: 1 (4) E-->A; 3 (3) J-->G; 15 (2) A-->C; 24 (4) U-->Y; 39 (4) G==>K; 77 (3) M-->P; 85 (12) Y-->M; 86 (20) U-->A; 94 (10) A==>K; 104 (16) Y-->I; 113 (5) P-->U; 127 (4) K-->G; 133 (2) G-->I; 144 (4) M==>I; 146 (8) Y==>Q; 157 (15) F-->U; 178 (9) J-->A; 181 (8) M==>U; 183 (1) C-->A; 201 (10) P-->F; 210 (8) Y-->Q; 214 (9) P-->Y; 231 (6) G-->A; 241 (4) G==>K; 245 (5) F-->A; 248 (8) M-->U; 261 (3) M-->P; 267 (4) Y-->U; 268 (9) J-->A; 279 (4) Q-->U; 283 (2) S==>U; 284 (3) M-->P; 285 (2) K-->I; 290 (10) A-->K; 292 (5) F==>K; 294 (10) A-->K; 299 (4) Y-->U; 311 (1) A-->B; 313 (1) G-->A; 317 (1) A-->C; 377 (1) G-->A; 392 (1) A-->C; 413 (1) C-->A; 495 (1) C-->A; 542 (1) C-->T; 550 (1) C-->A; 563 (1) T-->C; 620 (1) C-->T; 650 (1) A-->C; 659 (1) A-->G; 665 (1) C-->A; 707 (1) C-->T; 761 (1) A-->C; 814 (1) T-->C; 930 (1) A-->G; 1008 (1) T-->C; 1010 (1) T-->A; 1109 (1) T-->C; 1144 (1) A-->C; 1216 (1) A-->T; 1217 (1) C-->T; 1368 (1) T-->C; 1422 (1) C-->A; 1495 (1) T-->C; 1573 (1) T-->C; 1674 (1) T-->C; 1939 (1) C-->T; 2157 (1) C-->A; 2381 (1) T-->C; 2431 (1) T-->C; 2484 (1) T-->C; 2522 (1) T-->C; 2642 (1) C-->A.
DELTRAN: 2 (2) E==>G; 31 (12) A-->M; 36 (2) U==>S; 39 (5) K==>P; 45 (4) Y-->U; 53 (11) P-->E; 54 (4) E-->A; 80 (5) K-->P; 94 (2) K==>M; 102 (2) S-->Q; 103 (4) E==>A; 105 (6) G-->A; 115 (5) A-->F; 121 (7) F==>M; 136 (2) K==>M; 144 (8) I==>A; 145 (6) G==>A; 146 (1) Q==>P; 153 (8) Y==>Q; 162 (5) A-->F; 181 (4) U==>Y; 219 (7) Q==>J; 241 (5) K==>P; 249 (4) Y==>U; 266 (2) U==>S; 271 (4) U==>Y; 274 (6) A-->G; 278 (2) M-->K; 283 (4) U==>Y; 289 (14) K==>Y; 292 (14) K==>Y; 293 (5) F==>K; 309 (10) A==>K; 368 (1) T-->C; 387 (1) C-->T; 392 (1) A-->C; 477 (1) C-->A; 479 (1) A-->G; 485 (1) C-->T; 495 (1) C-->A; 542 (1) C-->T; 650 (1) A-->C; 665 (1) C-->A; 700 (1) C-->T; 761 (1) A-->C; 1015 (1) A==>T; 1071 (1) C==>T; 1494 (1) G-->A; 1546 (1) C==>T; 1735 (1) T-->C; 1911 (1) C-->T; 2070 (1) T-->C; 2524 (1) A-->C.

Branch 4
ACCTRAN: 2 (3) D==>G; 3 (2) G-->E; 4 (1) L==>M; 9 (1) K-->J; 10 (2) L-->J; 12 (2) H==>J; 14 (1) C-->B; 23 (8) M-->E; 31 (12) A-->M; 36 (2) U-->S; 39 (5) K-->P; 53 (15) P-->A; 54 (4) E-->A; 80 (5) K-->P; 85 (3) M-->J; 94 (2) K==>M; 100 (4) E-->A; 101 (4) E-->A; 103 (4) E-->A; 105 (6) G-->A; 110 (5) P-->K; 121 (7) F-->M; 123 (5) P-->U; 136 (2) K-->M; 144 (8) I-->A; 145 (6) G-->A; 149 (5) A-->F; 153 (4) Y-->U; 159 (5) K-->F; 162 (5) A==>F; 180 (3) P-->M; 181 (4) U-->Y; 188 (4) U-->Y; 189 (4) U-->Y; 190 (9) P-->Y; 191 (6) E-->K; 210 (8) Q-->I; 219 (9) S==>J; 220 (5) F-->A; 226 (8) M-->U; 241 (5) K-->P; 242 (8) A-->I; 257 (4) U==>Q; 266 (2) U-->S; 271 (4) U-->Y; 274 (6) A==>G; 278 (2) M-->K; 283 (4) U-->Y; 285 (2) I-->G; 289 (14) K-->Y; 292 (14) K-->Y; 308 (8) I-->A; 309 (6) A-->G; 368 (1) T-->C; 387 (1) C-->T; 404 (1) T-->C; 477 (1) C-->A; 479 (1) A-->G; 485 (1) C-->T; 570 (1) T-->A; 623 (1) C-->T; 674 (1) C-->T; 708 (1) T-->C; 725 (1) T-->C; 749 (1) T-->C; 813 (1) T-->C; 998 (1) T-->C; 1005 (1) T-->C; 1015 (1) A-->T; 1327 (1) C-->T; 1392 (1) C-->T; 1399 (1) A-->G; 1426 (1) C-->T; 1494 (1) G-->A; 1508 (1) T-->C; 1546 (1) C-->T; 1735 (1) T-->C; 1914 (1) A-->G; 2070 (1) T-->C; 2524 (1) A-->C; 2553 (1) T-->C.
DELTRAN: 1 (8) A==>I; 2 (6) G==>M; 4 (5) M==>R; 5 (7) I==>P; 7 (5) G==>L; 9 (2) J-->H; 11 (1) G==>H; 12 (3) J==>M; 13 (8) H==>P; 39 (1) P-->Q; 44 (6) A-->G; 71 (8) A==>I; 94 (12) M==>Y; 106 (11) F==>Q; 127 (10) K==>U; 129 (8) A==>I; 133 (4) I==>E; 143 (6) Y-->S; 157 (8) U-->M; 162 (11) F==>Q; 179 (8) K-->S; 203 (9) P==>Y; 204 (6) A==>G; 210 (8) I-->A; 216 (6) K-->Q; 218 (4) Y-->U; 219 (5) J==>E; 227 (2) K-->M; 230 (4) U-->Y; 231 (14) G==>U; 253 (3) P-->M; 257 (4) Q==>M; 268 (3) J==>M; 274 (14) G==>U; 278 (5) K-->F; 287 (4) U-->Y; 288 (3) M==>P; 290 (5) K==>P; 294 (1) G-->F; 306 (4) Y==>U; 307 (8) Y-->Q; 332 (1) A-->G; 410 (1) C-->T; 653 (1) A==>G; 1106 (1) A-->G; 1109 (1) C-->T; 1214 (1) C-->T; 1215 (1) A-->C; 1347 (1) C-->A; 1392 (1) C-->T; 2525 (1) T-->C.

Branch 5
ACCTRAN: 1 (8) A-->I; 2 (6) G==>M; 4 (5) M==>R; 5 (7) I-->P; 7 (5) G-->L; 9 (2) J-->H; 11 (1) G-->H; 12 (4) J-->N; 13 (8) H==>P; 39 (1) P-->Q; 43 (9) P-->Y; 44 (6) A==>G; 45 (4) Y-->U; 69 (5) F-->A; 71 (8) A-->I; 94 (12) M-->Y; 95 (4) Y-->U; 102 (2) S-->Q; 106 (11) F-->Q; 115 (5) A-->F; 116 (3) P-->S; 117 (2) K-->M; 127 (14) G-->U; 129 (8) A-->I; 133 (4) I-->E; 146 (1) Q-->P; 153 (4) U-->Q; 157 (8) U==>M; 158 (6) Y-->S; 159 (5) F-->A; 162 (11) F==>Q; 170 (3) S-->P; 179 (8) K-->S; 201 (1) F-->E; 203 (9) P-->Y; 204 (6) A-->G; 210 (8) I-->A; 216 (6) K==>Q; 219 (5) J-->E; 224 (5) F-->K; 227 (2) K-->M; 230 (4) U-->Y; 231 (20) A-->U; 257 (4) Q-->M; 267 (4) U-->Y; 268 (12) A-->M; 269 (4) U-->Y; 274 (14) G-->U; 278 (10) K-->A; 281 (3) F-->I; 287 (4) U-->Y; 288 (11) E-->P; 290 (5) K-->P; 293 (7) F-->M; 294 (5) K-->F; 296 (2) K-->M; 306 (4) Y-->U; 307 (8) Y-->Q; 309 (6) G-->M; 332 (1) A-->G; 410 (1) C-->T; 498 (1) T-->C; 573 (1) C-->A; 620 (1) T-->C; 696 (1) T-->C; 700 (1) C-->T; 713 (1) T-->C; 740 (1) T-->C; 1071 (1) C-->T; 1091 (1) T-->C; 1106 (1) A-->G; 1109 (1) C-->T; 1214 (1) C-->T; 1215 (1) A-->C; 1347 (1) C-->A; 1911 (1) C-->T; 2236 (1) C-->T; 2525 (1) T-->C.
DELTRAN: 2 (2) M==>O; 4 (1) R==>S; 5 (1) P-->Q; 7 (1) L-->M; 8 (2) Q-->S; 13 (1) P==>Q; 30 (4) Y==>U; 39 (4) Q-->U; 44 (6) G==>M; 77 (9) P==>Y; 79 (10) A==>K; 104 (4) I==>M; 121 (8) M-->U; 125 (10) K==>A; 131 (6) Y-->S; 133 (4) E-->A; 134 (8) Y-->Q; 146 (3) P-->M; 151 (3) P==>S; 153 (1) Q-->P; 157 (2) M==>K; 162 (4) Q==>U; 169 (12) A-->M; 171 (16) A==>Q; 190 (5)

P==>K; 216 (8) Q==>Y; 219 (4) E-->A; 223 (12) Y==>M; 226 (4) U-->Q; 229 (13) F==>S; 235 (15) P-->A; 285 (4) I==>M; 397 (1) C-->T; 417 (1) A==>T; 426 (1) C==>A; 428 (1) C==>T; 479 (1) G-->A; 498 (1) T-->C; 573 (1) C-->A; 615 (1) C==>T; 626 (1) A==>C; 644 (1) C-->T; 2078 (1) C-->T; 2236 (1) C-->T.

Branch 6
ACCTRAN: 2 (1) M-->N; 4 (1) R-->S; 7 (1) L-->M; 8 (2) Q-->S; 30 (4) Y-->U; 33 (6) S-->Y; 39 (4) Q-->U; 51 (4) U-->Y; 76 (4) U-->Y; 84 (4) Y-->U; 85 (5) J-->E; 97 (10) K-->A; 102 (6) Q-->K; 104 (4) I-->M; 106 (4) Q-->U; 113 (12) U-->I; 114 (6) K-->E; 115 (3) F-->I; 121 (8) M-->U; 125 (10) K-->A; 131 (6) Y-->S; 133 (4) E-->A; 143 (6) Y-->S; 146 (3) P-->M; 162 (4) Q-->U; 169 (8) A-->I; 190 (14) Y-->K; 216 (8) Q-->Y; 218 (4) Y-->U; 219 (4) E-->A; 223 (9) Y-->P; 229 (13) F-->S; 249 (4) Y-->U; 253 (3) P-->M; 261 (3) P-->M; 265 (1) F-->G; 277 (4) U-->Y; 285 (6) G-->M; 290 (5) P-->U; 299 (4) U-->Y; 397 (1) C-->T; 417 (1) A-->T; 426 (1) C-->A; 428 (1) C-->T; 479 (1) G-->A; 615 (1) C-->T; 626 (1) A-->C; 644 (1) C-->T; 653 (1) A-->G; 659 (1) G-->A; 1082 (1) C-->T; 1393 (1) T-->C; 1887 (1) T-->C; 2078 (1) C-->T.
DELTRAN: 3 (1) E-->D; 24 (4) Y-->U; 25 (4) Y==>U; 70 (4) A-->E; 170 (6) S==>Y; 180 (12) M-->Y; 201 (3) F==>I; 218 (2) U-->S; 229 (6) S-->Y; 241 (1) P-->Q; 358 (1) C-->T; 707 (1) T==>C; 746 (1) A-->G; 994 (1) G==>A; 1082 (1) C-->T; 1392 (1) T-->C; 1393 (1) T-->C; 1499 (1) C==>T; 1566 (1) T-->C; 2079 (1) C-->T.

Branch 7
ACCTRAN: 5 (1) P-->Q; 23 (6) E-->K; 24 (4) Y-->U; 41 (2) E-->G; 44 (6) G-->M; 45 (5) U-->P; 53 (4) A-->E; 70 (4) A-->E; 77 (9) P-->Y; 79 (10) A-->K; 124 (4) U-->Q; 134 (8) Y==>Q; 143 (8) S-->K; 149 (5) F-->A; 150 (8) Q-->Y; 151 (6) M-->S; 153 (8) Q-->I; 157 (12) M-->A; 169 (4) I==>M; 170 (9) P-->Y; 171 (16) A-->Q; 177 (3) P-->M; 180 (12) M-->Y; 201 (4) E-->I; 218 (2) U-->S; 223 (3) P-->M; 226 (4) U-->Q; 235 (15) P-->A; 241 (1) P-->Q; 248 (4) U-->Y; 249 (8) U-->M; 269 (4) Y-->U; 285 (4) M-->Q; 994 (1) G-->A; 1327 (1) T-->C; 1392 (1) T-->C; 1499 (1) C-->T; 1566 (1) T-->C; 2079 (1) C-->T; 2089 (1) C-->T.
DELTRAN: 6 (2) Q-->S; 23 (14) K-->Y; 24 (8) U-->M; 40 (4) A-->E; 71 (2) I-->K; 85 (6) J==>P; 97 (2) K==>M; 102 (8) Q==>Y; 113 (8) Q==>Y; 114 (2) K==>M; 115 (5) F==>A; 127 (4) U-->Y; 134 (8) Q==>I; 135 (8) I==>A; 151 (6) S-->Y; 162 (4) U-->Y; 169 (12) M==>Y; 218 (14) S-->E; 226 (6) Q-->K; 231 (4) U-->Y; 253 (2) M==>K; 265 (5) F==>A; 274 (4) U-->Y; 279 (4) U-->Y; 294 (5) F==>K; 307 (1) Q==>P; 904 (1) G==>A; 1008 (1) C==>T; 1236 (1) A-->G; 1398 (1) T-->C; 1399 (1) G==>A; 1422 (1) A==>T; 1546 (1) T==>C; 1728 (1) A==>T; 1860 (1) C==>A; 1908 (1) A==>C; 2078 (1) T-->C; 2089 (1) C-->T; 2101 (1) A-->G; 2113 (1) T-->C; 2231 (1) A==>G; 2236 (1) T==>C; 2382 (1) T-->C; 2486 (1) T==>C; 2504 (1) C-->T.

Branch 8
ACCTRAN: 2 (1) N-->O; 3 (1) E-->D; 6 (2) Q-->S; 12 (1) N-->M; 13 (1) P-->Q; 23 (14) K-->Y; 24 (8) U-->M; 25 (4) Y-->U; 40 (4) A-->E; 70 (1) E-->F; 71 (12) I-->U; 84 (4) U-->Y; 85 (11) E-->P; 97 (12) A-->M; 102 (14) K-->Y; 113 (16) I-->Y; 114 (11) E-->P; 115 (8) I-->A; 116 (3) S-->P; 117 (2) M-->K; 123 (4) U-->Y; 127 (4) U-->Y; 134 (8) Q-->I; 135 (8) I-->A; 151 (6) S-->Y; 158 (6) S-->Y; 162 (4) U-->Y; 169 (12) M-->Y; 171 (8) Q-->Y; 201 (4) I-->M; 214 (4) Y-->U; 218 (14) S-->E; 224 (5) K-->F; 226 (6) Q-->K; 229 (6) S-->Y; 231 (4) U-->Y; 242 (8) I-->A; 253 (2) M-->K; 257 (12) M-->Y; 265 (6) G-->A; 274 (4) U-->Y; 278 (20) A-->U; 279 (4) U-->Y; 281 (3) I-->F; 290 (5) U-->P; 294 (5) F-->K; 304 (4) A-->E; 307 (1) Q-->P; 309 (2) M-->K; 352 (1) G-->A; 358 (1) C-->T; 375 (1) C-->T; 399 (1) G-->A; 485 (1) T-->C; 488 (1) C-->G; 542 (1) T-->C; 594 (1) T-->C; 668 (1) C-->T; 674 (1) T-->C; 696 (1) C-->T; 707 (1) T-->C; 710 (1) A-->C; 740 (1) C-->T; 746 (1) A-->G; 904 (1) G-->A; 943 (1) T-->C; 1008 (1) C-->T; 1236 (1) A-->G; 1369 (1) A-->T; 1398 (1) T-->C; 1399 (1) G-->A; 1422 (1) A-->T; 1546 (1) T-->C; 1728 (1) A-->T; 1860 (1) C-->A; 1908 (1) A-->C; 2078 (1) T-->C; 2101 (1) A-->G; 2113 (1) T-->C; 2231 (1) A-->G; 2236 (1) T-->C; 2382 (1) T-->C; 2486 (1) T-->C; 2504 (1) C-->T.
DELTRAN: 1 (4) I==>M; 2 (2) O-->Q; 4 (2) S==>U; 5 (6) Q==>W; 9 (1) H-->G; 10 (5) J-->E; 11 (8) H-->P; 13 (3) Q-->T; 30 (4) U==>Y; 31 (3) M==>P; 41 (6) G==>A; 44 (12) M==>Y; 75 (3) M-->P; 131 (18) S==>A; 142 (8) Y==>Q; 143 (6) S==>Y; 148 (14) Y==>K; 160 (4) Y-->U; 177 (3) M-->P; 179 (6) S==>Y; 182 (2) M==>K; 189 (8) U-->M; 190 (6) K-->E; 204 (18) G==>Y; 223 (12) M==>A; 227 (3) M-->P; 232 (20) A==>U; 234 (16) Y==>I; 238 (4) Y-->U; 261 (3) M-->J; 266 (8) S==>K; 268 (4) M-->Q; 277 (4) Y==>U; 283 (4) Y==>U; 285 (2) M==>K; 288 (9) P==>Y; 375 (1) C-->T; 399 (1) G-->A; 411 (1) C-->T; 430 (1) A-->G; 447 (1) T-->C; 485 (1) T-->C; 488 (1) C-->G; 512 (1) C-->T; 537 (1) C-->T; 542 (1) T-->C; 557 (1) A-->G; 596 (1) A-->G; 599 (1) C-->T; 605 (1) C-->T; 635 (1) T-->C; 650 (1) C-->G; 656 (1) C-->T; 700 (1) T-->C; 719 (1) A-->G; 725 (1) C-->T; 758 (1) T-->C; 1369 (1) A-->T; 1426 (1) T==>C; 1600 (1) T==>C.

Branch 9
ACCTRAN: 1 (4) I-->M; 2 (2) O-->Q; 4 (2) S-->U; 5 (4) Q-->U; 10 (5) J-->E; 11 (8) H==>P; 13 (3) Q==>T; 30 (4) U-->Y; 44 (12) M-->Y; 75 (12) M-->Y; 97 (12) M-->Y; 100 (10) A-->K; 111 (6) E-->K; 142 (8) Y-->Q; 143 (14) K-->Y; 177 (3) M==>P; 179 (6) S-->Y; 182 (2) M-->K; 204 (18) G-->Y; 238 (4) Y==>U; 268 (4) M-->Q; 283 (4) Y-->U; 285 (11) Q-->F; 288 (9) P-->Y; 411 (1) C-->T; 430 (1) A-->G; 447 (1) T-->C; 512 (1) C-->T; 532 (1) T-->A; 537 (1) C-->T; 538 (1) T-->G; 539 (1) A-->G; 557 (1) A-->G; 596 (1) A-->G; 599 (1) C-->T; 605 (1) C-->T; 630 (1) T-->G; 635 (1) T-->C; 650 (1) C-->G; 656 (1) C-->T; 700 (1) T-->C; 719 (1) A-->G; 725 (1) C-->T; 758 (1) T-->C; 1426 (1) T-->C; 1548 (1) C-->A; 1600 (1) T-->C.
DELTRAN: 11 (3) P==>S; 13 (3) T==>W; 85 (5) P-->U; 116 (5) P==>U; 177 (9) P==>Y; 224 (12) I==>U; 238 (5) U==>P; 241 (4) Q-->U; 242 (20) A==>U; 281 (2) I==>K; 332 (1) G-->A; 347 (1) T==>C; 396 (1) A-->C; 421 (1) C==>A; 452 (1) C==>A; 453 (1) C==>T; 459 (1) C==>T; 509 (1) C==>T; 515 (1) A==>G; 532 (1) T-->A; 544 (1) T==>C; 560 (1) C==>T; 578 (1) A-->G; 630 (1) T-->G; 939 (1) A==>G; 1076 (1) C==>A; 1236 (1) G-->A; 1398 (1) C-->T; 1548 (1) C-->A; 2033 (1) A==>G; 2467 (1) T-->C.

Branch 10
ACCTRAN: 2 (2) Q-->S; 4 (1) U-->V; 5 (2) U-->W; 9 (1) H-->G; 11 (8) P-->X; 13 (3) T-->W; 24 (2) M-->K; 31 (3) M-->P; 36 (6) S-->M; 41 (6) G-->A; 70 (5) F-->A; 85 (5) P-->U; 95 (4) U-->Y; 98 (4) A-->E; 116 (9) P-->Y; 117 (6) K-->E; 123 (4) Y-->U; 131 (18)

S-->A; 136 (4) M-->I; 148 (18) Y-->G; 157 (10) A-->K; 160 (4) Y-->U; 171 (16) Y-->I; 177 (9) P-->Y; 189 (12) Y-->M; 190 (6) K-->E; 191 (6) K-->E; 201 (7) M-->F; 223 (12) M-->A; 224 (15) F-->U; 227 (3) M-->P; 232 (20) A-->U; 234 (20) Y-->E; 238 (5) U-->P; 241 (4) Q-->U; 242 (20) A-->U; 248 (4) Y-->U; 249 (8) M-->U; 257 (4) Y-->U; 261 (3) M-->J; 266 (8) S-->K; 277 (4) Y-->U; 278 (20) U-->A; 281 (5) F-->K; 283 (16) U-->E; 284 (11) P-->E; 293 (2) M-->K; 296 (2) M-->K; 332 (1) G-->A; 347 (1) T-->C; 352 (1) A-->G; 396 (1) A-->C; 421 (1) C-->A; 452 (1) C-->A; 453 (1) C-->T; 459 (1) C-->T; 509 (1) C-->T; 515 (1) A-->G; 544 (1) T-->C; 560 (1) C-->T; 578 (1) A-->G; 594 (1) C-->T; 668 (1) T-->C; 674 (1) C-->T; 710 (1) C-->A; 740 (1) T-->C; 939 (1) A-->G; 943 (1) C-->T; 1075 (1) C-->T; 1076 (1) C-->A; 1236 (1) G-->A; 1398 (1) C-->T; 2033 (1) A-->G; 2061 (1) C-->T; 2325 (1) A-->G; 2467 (1) T-->C.
DELTRAN: 6 (1) S==>R; 25 (5) U-->P; 46 (4) A-->E; 51 (4) Y==>U; 69 (10) A==>K; 80 (5) P==>U; 86 (4) A==>E; 97 (2) M==>K; 104 (6) M-->S; 106 (1) Q-->P; 129 (16) I-->Y; 134 (2) I==>G; 139 (1) B==>A; 150 (6) Q-->K; 157 (5) K-->P; 160 (15) U-->F; 167 (24) A==>Y; 178 (4) A==>E; 187 (9) Y-->P; 188 (16) U-->E; 189 (8) M-->E; 209 (4) Q-->U; 214 (2) U==>S; 222 (8) A==>I; 226 (10) K-->A; 229 (8) Y==>Q; 247 (4) Y==>U; 248 (8) U-->M; 261 (5) J-->E; 270 (9) P==>Y; 275 (18) A-->S; 276 (6) A-->G; 290 (9) P==>Y; 299 (4) Y-->U; 309 (5) K-->P; 362 (1) A==>G; 431 (1) C==>T; 479 (1) A-->G; 537 (1) T-->C; 540 (1) A-->G; 545 (1) A==>G; 617 (1) A==>G; 672 (1) A-->T; 764 (1) C==>T; 1008 (1) T==>C; 2073 (1) A==>G; 2078 (1) C==>T.

Branch 11
ACCTRAN: 11 (9) P-->Y; 12 (4) M-->Q; 13 (3) T-->W; 33 (12) Y==>M; 45 (15) P-->A; 70 (5) F-->A; 71 (20) U==>A; 79 (14) K-->Y; 80 (3) P==>M; 85 (9) P-->Y; 95 (4) U-->Y; 100 (14) K==>Y; 104 (12) M-->A; 110 (2) K-->M; 111 (2) K-->M; 114 (3) P-->M; 116 (9) P-->Y; 117 (10) K==>A; 123 (24) Y-->A; 124 (4) Q==>M; 129 (8) I==>A; 134 (16) I==>Y; 142 (16) Q-->A; 171 (24) Y==>A; 177 (9) P-->Y; 182 (10) K==>A; 201 (12) M==>A; 212 (20) E-->Y; 214 (4) U==>Y; 224 (19) F-->Y; 238 (20) U==>A; 241 (8) Q-->Y; 242 (24) A-->Y; 257 (12) Y-->M; 267 (8) Y-->Q; 269 (8) U-->M; 270 (3) P-->M; 278 (20) U-->A; 281 (19) F-->Y; 283 (20) U==>A; 284 (15) P==>A; 285 (5) F==>A; 290 (3) P==>M; 294 (10) K==>A; 332 (1) G-->A; 347 (1) T-->C; 352 (1) A-->G; 396 (1) A-->C; 417 (1) T-->A; 421 (1) C-->A; 452 (1) C-->A; 453 (1) C-->T; 459 (1) C-->T; 509 (1) C-->T; 515 (1) A-->G; 540 (1) A-->T; 544 (1) T-->C; 551 (1) A-->G; 560 (1) C-->T; 571 (1) C-->T; 572 (1) C-->A; 578 (1) A-->G; 594 (1) C-->T; 659 (1) A-->G; 668 (1) T-->C; 674 (1) C-->T; 710 (1) C-->A; 728 (1) C-->T; 740 (1) T-->C; 749 (1) C-->T; 931 (1) C-->A; 932 (1) C-->A; 933 (1) C-->A; 934 (1) C-->A; 935 (1) C-->A; 937 (1) C-->A; 939 (1) A-->G; 943 (1) C-->T; 1075 (1) C-->T; 1076 (1) C-->A; 1236 (1) G-->A; 1320 (1) A-->G; 1392 (1) C-->G; 1397 (1) C-->G; 1398 (1) C-->T; 1422 (1) T-->C; 1574 (1) C-->A; 2033 (1) A-->G; 2061 (1) C-->T; 2325 (1) A-->G; 2467 (1) T-->C.
DELTRAN: 33 (12) Y==>M; 71 (10) K==>A; 75 (9) P-->Y; 79 (14) K-->Y; 80 (3) P==>M; 85 (4) U-->Y; 97 (12) M-->Y; 100 (24) A==>Y; 116 (4) U-->Y; 117 (10) K==>A; 124 (8) U==>M; 129 (8) I==>A; 134 (16) I==>Y; 171 (16) Q==>A; 182 (10) K==>A; 188 (4) U-->Y; 201 (8) I==>A; 214 (4) U==>Y; 224 (4) U-->Y; 238 (15) P==>A; 278 (5) F-->A; 281 (14) K-->Y; 283 (20) U==>A; 284 (15) P==>A; 285 (10) K==>A; 290 (3) P==>M; 294 (10) K==>A.

Branch 12
3 (1) E-->D; 7 (12) M==>Y; 8 (5) S==>X; 9 (9) H==>Q; 12 (1) N-->M; 23 (6) E-->K; 24 (4) Y-->U; 25 (9) Y-->P; 46 (8) A==>I; 53 (4) A-->E; 70 (4) A-->E; 71 (4) I==>E; 75 (12) M-->Y; 111 (6) E-->K; 124 (4) U-->Q; 135 (7) I==>P; 141 (6) Y==>S; 143 (8) S-->K; 170 (9) P-->Y; 175 (4) Y==>U; 177 (3) P-->M; 179 (2) S-->U; 180 (12) M-->Y; 201 (4) E-->I; 203 (4) Y==>U; 209 (8) Q==>I; 218 (2) U-->S; 221 (21) Y==>D; 229 (6) S-->Y; 239 (4) A==>E; 240 (4) A==>E; 241 (1) P-->Q; 242 (4) I==>M; 249 (8) U-->M; 257 (12) M==>A; 261 (6) M==>G; 269 (4) Y-->U; 274 (8) U==>M; 281 (2) I==>K; 285 (4) M-->Q; 289 (4) Y==>U; 292 (9) Y==>P; 293 (2) M-->K; 296 (4) M==>I; 332 (1) G-->A; 352 (1) G-->A; 358 (1) C-->T; 362 (1) A-->G; 373 (1) T-->C; 375 (1) C-->T; 380 (1) A-->G; 389 (1) C-->A; 399 (1) G-->A; 416 (1) C-->T; 419 (1) C-->T; 429 (1) A-->G; 443 (1) T-->C; 449 (1) C-->T; 485 (1) T-->C; 488 (1) C-->G; 493 (1) C-->A; 494 (1) C-->T; 496 (1) T-->C; 503 (1) C-->T; 506 (1) C-->T; 524 (1) A-->T; 532 (1) T-->G; 542 (1) T-->A; 567 (1) A-->G; 594 (1) T-->C; 614 (1) A-->C; 620 (1) C-->T; 630 (1) T-->G; 641 (1) A-->G; 649 (1) T-->C; 668 (1) C-->T; 674 (1) T-->C; 680 (1) C-->T; 686 (1) C-->T; 689 (1) T-->C; 692 (1) A-->G; 696 (1) C-->T; 698 (1) A-->G; 703 (1) C-->T; 707 (1) T-->C; 710 (1) A-->C; 719 (1) A-->T; 740 (1) C-->T; 746 (1) A-->G; 752 (1) A-->G; 764 (1) C-->T; 994 (1) G-->A; 1076 (1) C==>T; 1144 (1) C==>T; 1327 (1) T-->C; 1369 (1) A-->T; 1392 (1) T-->C; 1499 (1) C-->T; 1566 (1) T-->C; 1573 (1) C==>A; 1749 (1) T==>C; 1810 (1) C-->A; 1861 (1) T==>A; 2079 (1) C-->T; 2440 (1) C==>T; 2515 (1) A-->C.
DELTRAN: 7 (12) M==>Y; 8 (5) S==>X; 9 (9) H==>Q; 25 (5) U-->P; 46 (8) A==>I; 71 (4) I==>E; 75 (12) M-->Y; 84 (4) Y-->U; 85 (5) J-->E; 97 (10) K-->A; 102 (6) Q-->K; 106 (4) Q-->U; 111 (6) E-->K; 113 (8) Q-->I; 114 (6) K-->E; 115 (3) F-->I; 124 (4) U-->Q; 135 (7) I==>P; 141 (6) Y==>S; 143 (8) S-->K; 175 (4) Y==>U; 179 (2) S-->U; 203 (4) Y==>U; 209 (8) Q==>I; 221 (21) Y==>D; 239 (4) A==>E; 240 (4) A==>E; 242 (12) A==>M; 249 (8) U-->M; 257 (12) M==>A; 261 (6) M==>G; 265 (1) F-->G; 269 (4) Y-->U; 274 (8) U==>M; 281 (2) I==>K; 285 (4) M-->Q; 289 (4) Y==>U; 290 (5) P-->U; 292 (9) Y==>P; 296 (2) K==>I; 1076 (1) C==>T; 1144 (1) C==>T; 1369 (1) A-->T; 1573 (1) C==>A; 1749 (1) T==>C; 1861 (1) T==>A; 2440 (1) C==>T.

Branch 13
ACCTRAN: 1 (4) I==>M; 2 (2) M-->O; 3 (2) E-->G; 4 (2) R-->T; 5 (3) P-->S; 6 (1) Q-->P; 7 (1) L-->M; 8 (2) Q-->S; 9 (1) H-->G; 10 (4) J-->F; 13 (1) P-->Q; 17 (4) Y-->U; 18 (24) Y==>A; 26 (8) A==>I; 28 (4) Y-->U; 29 (9) Y-->P; 30 (9) Y==>P; 33 (6) S-->Y; 36 (6) S-->M; 39 (8) Q==>Y; 41 (6) E-->K; 44 (6) G-->M; 51 (4) U-->Y; 76 (4) U-->Y; 77 (9) P-->Y; 79 (12) A-->M; 80 (3) P-->M; 95 (2) U-->S; 97 (10) K-->A; 100 (24) A==>Y; 101 (24) A==>Y; 102 (6) Q-->K; 104 (16) I-->Y; 106 (4) Q-->U; 113 (14) U-->G; 114 (10) K-->A; 115 (19) F-->Y; 116 (6) S==>Y; 121 (12) M==>Y; 123 (4) U-->Y; 125 (10) K-->A; 127 (4) U-->Y; 129 (8) I-->Q; 131 (12) Y-->M; 133 (4) E-->A; 134 (12) Y-->M; 146 (15) P==>A; 149 (5) F-->A; 150 (8) Q-->Y; 151 (6) M-->S; 153 (12) Q-->E; 157 (12) M-->A; 160 (6) Y-->S; 162 (8) Q-->Y; 169 (12) A-->M; 170 (15) P==>A; 171 (16) A-->Q; 177 (5) P==>U; 188 (6) Y-->S; 189 (12) Y-->M; 190 (24) Y-->A; 191 (10) K==>A; 201 (4) E==>A; 204 (9) G==>P; 208 (4) U-->Q; 216 (8) Q-->Y; 219 (4) E-->A; 223 (24) Y==>A; 226 (20) U-->A; 227 (12) M==>Y; 229 (13) F-->S; 231 (4) U-->Y; 232 (18) A==>S; 234 (16) Y==>I; 235 (15) P-->A; 241 (11) P==>E; 242 (8) I-->A; 248 (4) U-->Y; 261 (3) P-->M; 265 (1) F-->G; 268 (12) M==>Y; 270 (9) P==>Y; 272 (24) A--

>Y; 274 (4) U-->Y; 275 (24) A-->Y; 282 (4) Y==>U; 284 (3) P-->M; 285 (6) G-->M; 288 (9) P==>Y; 290 (9) P==>Y; 291 (24) A==>Y; 299 (4) U-->Y; 309 (12) M==>Y; 397 (1) C-->T; 417 (1) A-->T; 421 (1) C==>A; 426 (1) C-->A; 428 (1) C-->A; 479 (1) G-->A; 485 (1) T-->A; 488 (1) C-->A; 531 (1) T-->C; 532 (1) T-->A; 542 (1) T-->C; 551 (1) A-->G; 570 (1) A==>T; 593 (1) C==>A; 615 (1) C-->T; 621 (1) A==>G; 623 (1) T==>C; 626 (1) A-->C; 629 (1) A==>G; 644 (1) C-->T; 671 (1) C==>A; 683 (1) A==>G; 708 (1) C==>T; 725 (1) C-->T; 902 (1) T==>C; 930 (1) G==>A; 988 (1) T==>G; 998 (1) C-->T; 1015 (1) T-->A; 1175 (1) T==>C; 1446 (1) T-->A; 1536 (1) T==>C; 2033 (1) A==>G; 2073 (1) A==>G; 2078 (1) C-->T; 2342 (1) A-->G; 2381 (1) C-->T; 2382 (1) T-->C; 2484 (1) C==>T; 2522 (1) C-->T.
DELTRAN: 1 (4) I==>M; 10 (3) J-->G; 18 (6) Y==>S; 26 (4) A==>E; 30 (2) U==>S; 39 (4) U==>Y; 97 (10) K-->A; 100 (18) A==>S; 101 (18) A==>S; 102 (4) Q-->M; 106 (2) Q-->S; 113 (6) Q-->K; 114 (4) K-->G; 116 (5) P==>U; 121 (4) U==>Y; 127 (4) U-->Y; 146 (4) M==>I; 153 (3) P-->M; 157 (10) K-->A; 158 (4) Y-->U; 160 (4) Y-->U; 162 (4) U-->Y; 170 (18) S==>A; 177 (6) M==>S; 188 (2) U-->S; 189 (8) U-->M; 190 (4) K-->G; 191 (4) E==>A; 201 (5) F==>A; 204 (9) G==>P; 223 (12) M==>A; 226 (16) Q-->A; 227 (12) M==>Y; 231 (4) U-->Y; 232 (15) A==>P; 234 (12) Y==>M; 241 (9) P==>G; 268 (6) M==>S; 270 (9) P==>Y; 274 (4) U-->Y; 275 (15) A-->P; 278 (5) F-->A; 282 (4) Y==>U; 288 (9) P==>Y; 290 (9) P==>Y; 291 (15) A==>P; 309 (10) K==>U; 421 (1) C==>A; 488 (1) C-->A; 532 (1) T-->A; 542 (1) T-->C; 570 (1) A==>T; 593 (1) C==>A; 621 (1) A==>G; 623 (1) T==>C; 629 (1) A==>G; 671 (1) C==>A; 683 (1) A==>G; 708 (1) C==>T; 725 (1) C-->T; 902 (1) T==>C; 930 (1) G==>A; 988 (1) T==>G; 1175 (1) T==>C; 1536 (1) T==>C; 2033 (1) A==>G; 2073 (1) A==>G; 2382 (1) T-->C; 2484 (1) C==>T.

Branch 14
ACCTRAN: 2 (6) O==>U; 4 (1) T==>U; 5 (3) S==>V; 14 (1) B-->C; 27 (4) Y==>U; 28 (2) U==>S; 52 (4) U==>Y; 53 (4) A-->E; 70 (6) A==>G; 71 (4) I-->M; 75 (6) M-->S; 85 (11) J==>U; 110 (10) K==>U; 111 (16) E==>U; 113 (6) G==>A; 118 (6) A==>G; 124 (4) U==>Y; 143 (8) Y-->Q; 152 (9) A==>J; 167 (24) A==>Y; 169 (6) M==>S; 179 (6) S==>Y; 180 (12) M-->Y; 188 (14) S==>E; 189 (12) M==>A; 209 (8) Q==>Y; 253 (3) P-->M; 277 (5) U==>P; 293 (8) M==>U; 304 (6) A==>G; 428 (1) A-->T; 430 (1) A-->G; 447 (1) T==>C; 452 (1) C==>T; 509 (1) C==>T; 512 (1) C-->T; 539 (1) A==>G; 575 (1) T==>C; 598 (1) C==>T; 609 (1) G==>A; 632 (1) C==>T; 650 (1) C-->G; 702 (1) A==>G; 904 (1) G==>A; 1015 (1) A-->C; 1082 (1) C-->T; 1380 (1) C==>T; 1392 (1) T-->C; 1393 (1) T-->C; 1411 (1) T-->A; 1485 (1) T==>C; 1566 (1) T-->C; 1572 (1) C-->A; 1575 (1) C-->A; 1618 (1) C==>A; 1771 (1) G==>A; 1783 (1) G==>A; 1810 (1) C==>T; 1914 (1) G==>A; 1946 (1) A==>C; 1955 (1) T==>A; 2079 (1) C-->T; 2157 (1) A==>G; 2300 (1) A-->C.
DELTRAN: 2 (6) O==>U; 4 (2) S==>U; 5 (5) Q==>V; 12 (1) M-->N; 17 (4) Y-->U; 18 (18) S-->A; 27 (4) Y==>U; 28 (6) Y==>S; 29 (9) Y-->P; 30 (3) S-->P; 36 (6) S-->M; 41 (4) G-->K; 52 (4) U==>Y; 70 (6) A==>G; 71 (4) I-->M; 75 (6) M-->S; 85 (11) J==>U; 110 (10) K==>U; 111 (16) E==>U; 113 (10) K==>A; 114 (6) G-->A; 117 (2) K-->M; 118 (6) A==>G; 123 (4) U-->Y; 124 (4) U==>Y; 143 (2) S-->Q; 152 (9) A==>J; 167 (24) A==>Y; 169 (6) M==>S; 179 (6) S==>Y; 180 (12) M-->Y; 188 (14) S==>E; 189 (12) M==>A; 190 (6) G-->A; 209 (8) Q==>Y; 214 (4) U-->Y; 224 (2) I-->K; 249 (4) U==>Y; 277 (9) Y==>P; 291 (9) P-->Y; 293 (10) K==>U; 304 (6) A==>G; 430 (1) A-->G; 447 (1) T==>C; 452 (1) C==>T; 509 (1) C==>T; 512 (1) C-->T; 531 (1) T-->C; 539 (1) A==>G; 575 (1) T==>C; 598 (1) C==>T; 609 (1) G==>A; 632 (1) C==>T; 653 (1) G==>A; 659 (1) A==>G; 702 (1) A==>G; 904 (1) G==>A; 1015 (1) T-->C; 1082 (1) C-->T; 1327 (1) C-->T; 1380 (1) C==>T; 1392 (1) T-->C; 1393 (1) T-->C; 1446 (1) T-->A; 1485 (1) T==>C; 1566 (1) T-->C; 1618 (1) C==>A; 1771 (1) G==>A; 1783 (1) G==>A; 1810 (1) C==>T; 1887 (1) C==>T; 1914 (1) G==>A; 1946 (1) A==>C; 1955 (1) T==>A; 2079 (1) C-->T; 2157 (1) A==>G.

Branch 15
ACCTRAN: 6 (4) P==>L; 14 (1) B==>A; 52 (14) U-->G; 75 (6) M-->G; 79 (4) M==>Q; 84 (4) Y-->U; 85 (9) J-->A; 102 (10) K-->A; 106 (4) U==>Y; 110 (10) K-->A; 111 (4) E-->A; 129 (8) Q==>Y; 131 (12) M==>A; 136 (12) M==>A; 153 (4) E==>A; 158 (8) S-->K; 174 (6) Y-->S; 177 (4) U-->Y; 178 (12) A==>M; 180 (6) M-->G; 205 (9) A-->J; 209 (8) Q==>I; 212 (4) E==>A; 214 (18) Y==>G; 225 (8) A-->I; 238 (14) Y==>K; 241 (4) E-->A; 249 (24) Y==>A; 253 (9) P==>Y; 265 (2) G-->I; 277 (4) U-->Y; 283 (8) Y==>Q; 284 (4) M==>I; 294 (5) F-->A; 296 (12) M==>Y; 306 (4) U==>Q; 373 (1) T==>C; 392 (1) C==>A; 420 (1) C==>A; 433 (1) T-->A; 451 (1) C==>A; 455 (1) A==>G; 459 (1) C==>T; 493 (1) C==>G; 496 (1) T==>C; 522 (1) A==>T; 537 (1) C==>A; 548 (1) C==>A; 602 (1) C==>T; 605 (1) C==>T; 636 (1) A==>G; 637 (1) C==>T; 653 (1) A-->G; 659 (1) G-->A; 723 (1) A==>G; 744 (1) A==>G; 755 (1) C==>A; 935 (1) C==>T; 980 (1) A==>G; 1044 (1) G==>A; 1131 (1) A==>T; 1147 (1) T==>C; 1212 (1) C==>T; 1253 (1) C==>T; 1327 (1) T-->C; 1331 (1) A==>G; 1369 (1) A==>G; 1391 (1) C==>T; 1394 (1) T==>C; 1398 (1) T==>C; 1399 (1) G==>A; 1423 (1) A==>T; 1433 (1) T==>G; 1471 (1) C==>T; 1482 (1) C==>T; 1548 (1) C==>T; 1740 (1) T==>A; 1779 (1) C-->A; 1781 (1) C-->A; 1887 (1) T-->C; 1909 (1) A==>G; 2089 (1) C-->T; 2160 (1) G==>A; 2431 (1) C==>A.
DELTRAN: 3 (2) E-->G; 6 (2) Q==>O; 9 (1) H-->G; 10 (1) G-->F; 14 (1) B==>A; 79 (6) K==>Q; 85 (5) J-->E; 100 (6) S-->Y; 101 (6) S-->Y; 106 (6) S==>Y; 115 (5) F-->K; 129 (12) I==>U; 131 (18) S==>A; 134 (4) Q-->M; 136 (12) M==>A; 150 (4) Q-->U; 153 (12) M==>A; 177 (2) S-->U; 178 (9) A==>J; 209 (8) Q==>I; 212 (4) E==>A; 214 (14) U==>G; 232 (3) P-->S; 234 (4) M-->I; 238 (12) Y==>M; 248 (4) U-->Y; 249 (20) U==>A; 253 (12) M==>Y; 268 (6) S-->Y; 283 (4) Y==>U; 284 (7) P==>I; 296 (14) K==>Y; 306 (4) U==>Q; 373 (1) T==>C; 392 (1) C==>A; 420 (1) C==>A; 451 (1) C==>A; 455 (1) A==>G; 459 (1) C==>T; 485 (1) T-->A; 493 (1) C==>G; 496 (1) T==>C; 522 (1) A==>T; 537 (1) C==>A; 548 (1) C==>A; 551 (1) A-->G; 602 (1) C==>T; 605 (1) C==>T; 636 (1) A==>G; 637 (1) C==>T; 696 (1) T-->C; 723 (1) A==>G; 744 (1) A==>G; 755 (1) C==>A; 935 (1) C==>T; 980 (1) A==>G; 998 (1) C-->T; 1015 (1) T-->A; 1044 (1) G==>A; 1131 (1) A==>T; 1147 (1) T==>C; 1212 (1) C==>T; 1253 (1) C==>T; 1331 (1) A==>G; 1369 (1) A==>G; 1391 (1) C==>T; 1394 (1) T==>C; 1398 (1) T==>C; 1399 (1) G==>A; 1423 (1) A==>T; 1433 (1) T==>G; 1471 (1) C==>T; 1482 (1) C==>T; 1548 (1) C==>T; 1740 (1) T==>A; 1909 (1) A==>G; 2089 (1) C-->T; 2160 (1) G==>A; 2342 (1) A-->G; 2381 (1) C-->T; 2431 (1) C==>A; 2522 (1) C-->T.

Branch 16
ACCTRAN: 3 (1) G==>H; 7 (11) M-->X; 8 (1) S-->R; 10 (2) F-->D; 12 (2) N-->L; 13 (1) Q-->R; 23 (4) E-->A; 24 (12) Y-->M; 29 (6) P==>J; 30 (6) P==>J; 31 (3) M==>J; 36 (7) M==>F; 40 (12) A==>M; 41 (10) K-->A; 45 (8) U==>M; 66 (24) A-->Y; 71 (2)

I==>G; 79 (2) Q==>S; 113 (4) G-->K; 135 (4) I-->M; 155 (9) Y-->P; 161 (5) A-->F; 169 (6) M-->G; 182 (7) M==>F; 209 (2) I-->G; 222 (6) A==>G; 224 (10) K-->A; 229 (6) S-->Y; 232 (6) S==>Y; 234 (2) I==>G; 258 (12) A-->M; 261 (4) M-->Q; 266 (18) S-->A; 279 (20) U-->A; 284 (4) I==>E; 285 (2) M==>K; 291 (9) Y-->P; 303 (24) Y-->A; 352 (1) G==>A; 371 (1) C==>T; 411 (1) C==>T; 429 (1) A==>G; 482 (1) C==>T; 692 (1) A==>T; 743 (1) C==>T; 746 (1) A-->G; 944 (1) A==>G; 1046 (1) G==>A; 1573 (1) C==>A; 1749 (1) T==>C; 2230 (1) A==>G.
DELTRAN: 3 (1) G==>H; 4 (1) S-->T; 5 (2) Q-->S; 17 (4) Y-->U; 18 (18) S-->A; 28 (4) Y-->U; 29 (15) Y==>J; 30 (9) S==>J; 31 (3) M==>J; 36 (13) S==>F; 40 (12) A==>M; 45 (8) U==>M; 71 (2) I==>G; 79 (2) Q==>S; 114 (6) G-->A; 117 (2) K-->M; 123 (4) U-->Y; 182 (7) M==>F; 190 (6) G-->A; 222 (6) A==>G; 229 (6) S-->Y; 232 (6) S==>Y; 234 (2) I==>G; 284 (4) I==>E; 285 (2) M==>K; 293 (2) K-->M; 352 (1) G==>A; 371 (1) C==>T; 411 (1) C==>T; 428 (1) T-->A; 429 (1) A==>G; 433 (1) T-->A; 482 (1) C==>T; 531 (1) T-->C; 692 (1) A==>T; 743 (1) C==>T; 746 (1) A-->G; 944 (1) A==>G; 1046 (1) G==>A; 1446 (1) T-->A; 1573 (1) C==>A; 1749 (1) T==>C; 2230 (1) A==>G.

Branch 17
ACCTRAN: 1 (8) A-->I; 2 (6) G-->M; 4 (5) M-->R; 5 (7) I-->P; 7 (5) G-->L; 9 (2) J-->H; 11 (1) G-->H; 12 (4) J-->N; 13 (8) H-->P; 23 (4) E-->A; 39 (1) P-->Q; 44 (6) A-->G; 46 (4) A-->E; 52 (16) U-->E; 71 (12) A-->M; 75 (3) M-->J; 80 (5) P-->U; 85 (9) J-->A; 94 (12) M-->Y; 97 (14) K-->Y; 98 (12) A==>M; 106 (11) F-->Q; 116 (3) P-->S; 117 (6) K-->Q; 127 (14) G-->U; 129 (8) A-->I; 133 (4) I-->E; 136 (3) M-->P; 143 (6) Y-->S; 150 (12) Q==>E; 152 (6) A-->G; 157 (8) U-->M; 158 (14) Y==>K; 159 (5) F-->A; 162 (11) F-->Q; 179 (8) K-->S; 180 (2) M-->K; 203 (9) P-->Y; 204 (6) A-->G; 208 (4) U-->Y; 210 (8) I-->A; 216 (6) K-->Q; 218 (6) Y-->S; 219 (5) J-->E; 225 (6) A-->G; 227 (2) K-->M; 230 (4) U-->Y; 231 (20) A-->U; 238 (4) Y-->U; 241 (1) P-->Q; 248 (8) U-->M; 253 (5) P-->K; 257 (4) Q-->M; 265 (5) F-->A; 266 (3) S-->P; 267 (4) U-->Y; 268 (12) A-->M; 269 (4) U-->Y; 274 (14) G-->U; 278 (10) K-->A; 279 (2) U-->S; 287 (4) U-->Y; 288 (11) E-->P; 290 (5) K-->P; 294 (10) K-->A; 296 (10) K-->U; 306 (4) Y-->U; 307 (8) Y-->Q; 313 (1) A==>G; 332 (1) A-->G; 398 (1) C==>T; 410 (1) C-->A; 430 (1) A-->G; 453 (1) C==>T; 511 (1) A-->C; 533 (1) C-->G; 544 (1) T==>C; 620 (1) T-->C; 635 (1) T==>C; 641 (1) A==>G; 653 (1) A-->G; 659 (1) G-->A; 696 (1) T-->C; 713 (1) T-->C; 737 (1) C==>T; 1002 (1) T-->C; 1091 (1) T-->C; 1106 (1) A-->G; 1109 (1) C-->T; 1141 (1) A-->G; 1214 (1) C-->T; 1215 (1) A-->C; 1347 (1) C-->A; 1393 (1) T-->C; 1749 (1) T==>C; 2089 (1) C-->T; 2504 (1) C-->T; 2525 (1) T-->C.
DELTRAN: 98 (4) A==>E; 150 (1) Q==>P; 158 (12) Y==>M; 242 (8) A-->I; 278 (5) F-->A; 313 (1) A==>G; 398 (1) C==>T; 430 (1) A-->G; 453 (1) C==>T; 544 (1) T==>C; 635 (1) T==>C; 641 (1) A==>G; 696 (1) T-->C; 737 (1) C==>T; 1749 (1) T==>C.

Branch 18
ACCTRAN: 12 (7) N-->U; 25 (8) Y-->Q; 40 (4) A-->E; 41 (4) E==>A; 44 (2) G-->I; 45 (9) Y-->P; 73 (6) A-->G; 79 (6) A-->G; 80 (4) U==>Y; 110 (6) K==>E; 115 (5) A-->F; 123 (4) U-->Y; 125 (5) K==>P; 148 (19) Y==>F; 174 (4) Y==>U; 182 (3) M==>P; 192 (8) A==>I; 193 (4) A==>E; 201 (1) F-->E; 212 (14) E==>S; 214 (6) Y==>S; 219 (4) E-->A; 229 (5) F-->A; 250 (12) Y-->M; 251 (12) A-->M; 253 (10) K==>A; 266 (3) P==>M; 274 (4) U-->Y; 297 (24) Y==>A; 307 (1) Q==>P; 347 (1) T-->C; 358 (1) C-->T; 362 (1) A-->G; 375 (1) C-->T; 380 (1) A-->G; 397 (1) C-->T; 399 (1) G-->A; 400 (1) C-->T; 405 (1) A-->G; 408 (1) A-->G; 412 (1) G-->T; 422 (1) T-->C; 429 (1) A-->G; 443 (1) T-->C; 446 (1) A-->C; 455 (1) A-->G; 478 (1) T-->C; 485 (1) T-->G; 498 (1) T-->C; 509 (1) C-->T; 512 (1) C-->T; 515 (1) A-->G; 530 (1) A-->G; 533 (1) G-->T; 534 (1) C-->T; 542 (1) T-->C; 545 (1) A-->C; 554 (1) A-->G; 566 (1) T-->C; 576 (1) A-->G; 581 (1) T-->C; 610 (1) T-->C; 647 (1) C-->T; 686 (1) C-->T; 904 (1) G==>A; 930 (1) G==>A; 1369 (1) A==>T; 1411 (1) T-->C; 1572 (1) C==>A; 1705 (1) C==>A; 1887 (1) T-->C; 1955 (1) T==>C; 2073 (1) A==>G; 2160 (1) G==>A; 2382 (1) T-->C; 2651 (1) A==>C; 2660 (1) T-->A.
DELTRAN: 23 (10) K-->A; 40 (4) A-->E; 41 (6) G==>A; 44 (2) G-->I; 45 (5) U-->P; 52 (16) U-->E; 53 (4) E-->A; 79 (6) A-->G; 80 (9) P==>Y; 85 (9) J-->A; 110 (6) K==>E; 123 (4) U-->Y; 125 (5) K==>P; 136 (3) M-->P; 146 (1) P==>Q; 148 (19) Y==>F; 152 (6) A-->G; 174 (4) Y==>U; 182 (3) M==>P; 188 (4) U-->Y; 189 (4) U-->Y; 190 (9) P-->Y; 191 (6) E-->K; 192 (8) A==>I; 193 (4) A==>E; 201 (1) F-->E; 208 (4) U-->Y; 212 (14) E==>S; 214 (2) U==>S; 219 (4) E-->A; 248 (8) U-->M; 253 (12) M==>A; 266 (6) S==>M; 274 (4) U-->Y; 285 (2) I-->G; 294 (5) F-->A; 297 (24) Y==>A; 307 (1) Q==>P; 904 (1) G==>A; 930 (1) G==>A; 1002 (1) T-->C; 1071 (1) T==>C; 1141 (1) A-->G; 1369 (1) A==>T; 1572 (1) C==>A; 1705 (1) C==>A; 1911 (1) T==>C; 1955 (1) T==>C; 2073 (1) A==>G; 2089 (1) C-->T; 2160 (1) G==>A; 2382 (1) T-->C; 2504 (1) C-->T; 2651 (1) A==>C.

Branch 19
ACCTRAN: 6 (5) Q==>L; 11 (3) H==>K; 46 (8) E==>M; 124 (5) U==>P; 125 (4) K-->G; 139 (1) B-->A; 143 (6) S==>M; 146 (4) Q-->M; 169 (16) A==>Q; 182 (6) M==>G; 212 (4) E==>A; 218 (3) S==>P; 239 (6) A==>G; 312 (1) C-->T; 335 (1) C-->T; 359 (1) C-->T; 361 (1) C-->T; 377 (1) A-->G; 396 (1) A-->G; 410 (1) A-->T; 417 (1) A-->C; 418 (1) C-->T; 437 (1) C-->T; 438 (1) A-->G; 440 (1) C-->T; 464 (1) A-->G; 476 (1) C-->T; 492 (1) A-->C; 495 (1) A-->C; 506 (1) C-->T; 511 (1) C-->G; 551 (1) A-->G; 569 (1) T-->C; 573 (1) C-->A; 602 (1) C-->T; 617 (1) A-->G; 636 (1) A-->G; 637 (1) C-->T; 638 (1) T-->C; 677 (1) T-->C; 683 (1) A-->G; 700 (1) C-->T; 701 (1) A-->C; 740 (1) T-->C; 761 (1) C-->T; 763 (1) G-->A; 936 (1) T==>C; 1071 (1) C-->T; 1144 (1) C==>T; 1387 (1) T==>C; 1536 (1) T==>C; 1731 (1) A==>G; 1783 (1) G==>A; 1907 (1) C==>T; 1911 (1) C-->T; 2065 (1) A==>T; 2078 (1) C-->T; 2079 (1) C-->T; 2101 (1) A-->G; 2439 (1) A==>G; 2484 (1) C==>T; 2692 (1) T-->C.
DELTRAN: 6 (5) Q==>L; 11 (3) H==>K; 45 (4) U==>Y; 46 (12) A==>M; 71 (4) I-->M; 75 (3) M-->J; 97 (14) K-->Y; 98 (8) E-->M; 115 (5) F==>A; 116 (3) P-->S; 117 (6) K-->Q; 124 (5) U==>P; 125 (4) K-->G; 143 (6) S==>M; 146 (3) P-->M; 149 (5) A-->F; 150 (11) P-->E; 151 (3) P-->M; 158 (2) M-->K; 169 (16) A==>Q; 180 (2) M-->K; 182 (6) M==>G; 212 (4) E==>A; 214 (4) U-->Y; 218 (5) U==>P; 225 (6) A-->G; 238 (4) Y-->U; 239 (6) A==>G; 241 (1) P-->Q; 265 (5) F-->A; 279 (2) U-->S; 296 (10) K-->U; 936 (1) T==>C; 1144 (1) C==>T; 1327 (1) C-->T; 1387 (1) T==>C; 1393 (1) T-->C; 1536 (1) T==>C; 1731 (1) A==>G; 1783 (1) G==>A; 1887 (1) C==>T; 1907 (1) C==>T; 2065 (1) A==>T; 2078 (1) C-->T; 2079 (1) C-->T; 2101 (1) A-->G; 2439 (1) A==>G; 2484 (1) C==>T.

Branch 20
ACCTRAN: 2 (3) D-->G; 5 (1) I-->H; 8 (2) Q-->O; 14 (2) C-->A; 31 (20) A-->U; 36 (5) U-->P; 39 (5) K-->P; 41 (14) E-->S; 45 (9) Y-->P; 49 (12) Y-->M; 53 (15) P-->A; 54 (4) E-->A; 69 (5) F-->A; 75 (8) M-->U; 80 (5) K-->P; 94 (2) K-->M; 95 (12) Y-->M; 100 (4) E-->A; 101 (4) E-->A; 102 (6) S-->M; 103 (4) E-->A; 104 (2) I-->G; 105 (6) G-->A; 106 (5) F-->A; 110 (11) P-->E; 115 (10) A==>K; 117 (10) K-->A; 121 (7) F-->M; 123 (5) P-->U; 125 (5) K-->P; 133 (2) I-->K; 135 (8) I-->A; 136 (2) K-->M; 144 (8) I-->A; 145 (6) G-->A; 146 (1) Q-->P; 151 (3) M-->P; 153 (8) Y-->Q; 159 (5) K-->F; 162 (5) A-->F; 167 (5) A-->F; 179 (10) K-->A; 181 (4) U-->Y; 188 (4) U-->Y; 189 (4) U-->Y; 190 (9) P-->Y; 191 (20) E-->Y; 192 (12) A-->M; 193 (12) A-->M; 194 (9) A-->J; 195 (9) A-->J; 201 (5) F-->A; 208 (20) U==>A; 209 (2) Q-->S; 219 (9) S-->J; 220 (5) F-->A; 224 (11) F==>Q; 226 (12) M==>Y; 227 (5) K-->F; 229 (5) F-->A; 230 (8) U-->M; 241 (5) K-->P; 242 (15) A==>P; 243 (5) A==>F; 248 (4) U-->Y; 249 (4) Y-->U; 261 (1) P-->Q; 266 (2) U-->S; 271 (4) U-->Y; 274 (6) A-->G; 277 (4) U-->Y; 278 (2) M-->K; 279 (4) U-->Y; 281 (5) F==>K; 283 (4) U-->Y; 289 (14) K-->Y; 292 (14) K-->Y; 293 (7) F-->M; 294 (5) K==>P; 296 (2) K==>I; 299 (4) U-->Q; 308 (8) I-->A; 309 (12) A-->M; 347 (1) T==>C; 358 (1) C-->T; 359 (1) C-->T; 368 (1) T-->C; 387 (1) C-->T; 396 (1) A-->G; 404 (1) T-->C; 438 (1) A==>G; 443 (1) T==>C; 477 (1) C-->A; 479 (1) A-->G; 485 (1) C-->T; 498 (1) T-->C; 509 (1) C==>T; 512 (1) C-->T; 532 (1) T-->C; 570 (1) T-->A; 573 (1) C-->A; 594 (1) T==>C; 644 (1) C-->T; 656 (1) C-->T; 700 (1) C-->T; 708 (1) T-->C; 725 (1) T-->C; 746 (1) A-->G; 749 (1) T-->C; 813 (1) T-->C; 1015 (1) A-->T; 1071 (1) C-->T; 1074 (1) A-->T; 1082 (1) C-->T; 1327 (1) C-->T; 1494 (1) G-->A; 1508 (1) T-->C; 1546 (1) C-->T; 1548 (1) C==>T; 1566 (1) T-->C; 1732 (1) A-->G; 1735 (1) T-->C; 1771 (1) G-->A; 1887 (1) T-->C; 1898 (1) A-->T; 1911 (1) C-->T; 2070 (1) T-->C; 2236 (1) C-->T; 2524 (1) A-->C.
DELTRAN: 102 (4) Q-->M; 115 (5) F==>K; 188 (4) U-->Y; 189 (4) U-->Y; 208 (16) U==>E; 214 (4) U-->Y; 224 (8) I==>Q; 226 (4) U==>Y; 242 (12) A==>M; 243 (5) A==>F; 268 (5) J-->E; 279 (4) U-->Y; 281 (2) I==>K; 294 (6) G==>M; 296 (2) K==>I; 347 (1) T==>C; 358 (1) C-->T; 438 (1) A==>G; 443 (1) T==>C; 498 (1) T-->C; 509 (1) C==>T; 594 (1) T==>C; 620 (1) C-->T; 746 (1) A-->G; 1082 (1) C-->T; 1091 (1) C-->T; 1548 (1) C==>T; 1566 (1) T-->C.

Branch 21
ACCTRAN: 4 (1) L-->M; 7 (3) G-->D; 8 (3) O-->L; 9 (3) K-->H; 10 (2) L-->J; 12 (2) H-->F; 13 (1) H-->G; 31 (4) U==>Y; 36 (3) P-->M; 39 (9) P-->Y; 45 (15) P==>A; 51 (4) U-->Y; 52 (4) U-->Y; 75 (4) U-->Y; 76 (4) U-->Y; 80 (9) P==>Y; 110 (4) E==>A; 111 (4) E==>A; 115 (2) K-->M; 123 (4) U-->Y; 124 (4) U-->Y; 125 (9) P==>Y; 146 (3) P-->M; 150 (8) Q-->Y; 157 (4) U-->Y; 159 (5) F-->A; 170 (18) S-->A; 177 (15) P-->A; 180 (3) P-->M; 216 (14) K==>Y; 224 (4) Q==>U; 227 (5) F==>A; 249 (2) U-->S; 251 (12) A-->M; 253 (3) P-->S; 254 (6) A-->G; 258 (4) A-->E; 269 (4) U-->Y; 278 (10) K-->A; 281 (2) K-->M; 287 (4) U-->Y; 288 (8) E-->M; 290 (2) K-->M; 293 (12) M-->Y; 375 (1) C-->T; 397 (1) C-->T; 615 (1) C-->T; 641 (1) A-->G; 686 (1) C-->T; 764 (1) C-->T; 801 (1) C==>T; 1073 (1) A==>G; 1214 (1) C-->T; 1215 (1) A-->C; 1393 (1) T-->C; 1572 (1) C==>A; 1955 (1) T==>C; 2692 (1) T==>C.
DELTRAN: 8 (1) Q-->P; 31 (12) M==>Y; 45 (20) U==>A; 80 (9) P==>Y; 110 (10) K==>A; 111 (4) E==>A; 125 (10) K==>U; 150 (4) Q-->U; 170 (3) S-->P; 179 (10) K-->A; 190 (9) P-->Y; 191 (20) E-->Y; 201 (5) F-->A; 208 (4) E-->A; 216 (14) K==>Y; 224 (4) Q==>U; 227 (10) K==>A; 396 (1) A-->G; 397 (1) C-->T; 512 (1) C-->T; 532 (1) T-->C; 573 (1) C-->A; 656 (1) C-->T; 801 (1) C==>T; 998 (1) C==>T; 1073 (1) A==>G; 1214 (1) C-->T; 1393 (1) T-->C; 1399 (1) G==>A; 1572 (1) C==>A; 1771 (1) G-->A; 1914 (1) G==>A; 1955 (1) T==>C; 2692 (1) T==>C.

Branch 22
ACCTRAN: 1 (4) A-->E; 2 (4) G-->K; 4 (2) M-->O; 5 (1) H-->I; 23 (3) M==>P; 32 (20) A==>U; 33 (6) S-->Y; 43 (11) P==>E; 94 (2) M==>K; 114 (5) K==>F; 116 (9) P==>Y; 121 (8) M-->U; 133 (10) K==>A; 137 (10) A==>K; 151 (9) P==>G; 158 (24) Y==>A; 162 (1) F==>G; 167 (5) F-->A; 219 (3) J-->G; 225 (15) A==>P; 283 (9) Y-->P; 284 (11) P==>E; 307 (8) Y-->Q; 410 (1) C-->T; 430 (1) A-->G; 451 (1) C-->T; 455 (1) A-->C; 496 (1) T-->C; 515 (1) A-->G; 543 (1) A-->C; 566 (1) T-->C; 575 (1) T-->C; 587 (1) A-->G; 596 (1) A-->G; 621 (1) A-->G; 653 (1) A-->G; 674 (1) C-->T; 695 (1) C-->T; 702 (1) A==>G; 713 (1) T-->C; 939 (1) A==>G; 1005 (1) T-->C; 1106 (1) A-->G; 1369 (1) A==>G; 1422 (1) A-->C; 1548 (1) T-->A; 1549 (1) A==>T; 1705 (1) C==>T; 1731 (1) A-->G; 1732 (1) G-->A; 1898 (1) T-->C; 2440 (1) C==>T; 2447 (1) C==>T.
DELTRAN: 1 (4) A-->E; 2 (2) G-->I; 4 (2) M-->O; 23 (5) K==>P; 32 (10) A==>K; 43 (20) Y==>E; 53 (4) E-->A; 94 (2) M==>K; 114 (5) K==>F; 116 (9) P==>Y; 121 (8) M-->U; 133 (8) I==>A; 137 (5) A==>F; 151 (9) P==>G; 158 (14) Y==>K; 162 (1) F==>G; 225 (8) A==>I; 242 (3) M-->P; 284 (3) P==>M; 294 (3) M-->P; 359 (1) C-->T; 410 (1) C-->T; 702 (1) A==>G; 939 (1) A==>G; 1074 (1) A-->T; 1106 (1) A-->G; 1215 (1) A-->C; 1369 (1) A==>G; 1426 (1) T==>C; 1549 (1) A==>T; 1705 (1) C==>T; 1898 (1) A-->C; 2440 (1) C==>T; 2447 (1) C==>T.

Branch 23
ACCTRAN: 3 (2) G-->E; 7 (3) D-->G; 8 (4) L-->P; 9 (6) H-->N; 10 (5) J-->O; 36 (12) M==>Y; 37 (4) A-->E; 39 (14) Y-->K; 52 (20) Y==>E; 75 (14) Y==>K; 76 (12) Y-->M; 84 (12) Y-->M; 85 (12) M-->A; 102 (8) M==>U; 104 (4) G-->K; 106 (12) A==>M; 109 (4) Y==>U; 115 (12) M-->A; 117 (10) A-->K; 123 (18) Y==>G; 124 (4) Y-->U; 125 (4) Y-->U; 135 (10) A==>K; 146 (2) M-->K; 150 (4) Y-->U; 152 (6) A-->G; 153 (8) Q-->Y; 159 (12) A-->M; 160 (9) Y-->P; 170 (15) A-->P; 177 (20) A-->U; 178 (15) A-->P; 180 (2) M-->K; 182 (12) M-->Y; 192 (8) M==>U; 193 (6) M==>S; 196 (4) A-->E; 210 (8) Q-->I; 230 (12) M==>A; 233 (9) Y-->P; 263 (5) A-->F; 264 (4) Y-->U; 268 (4) A-->E; 278 (15) A-->P; 281 (4) M-->Q; 287 (4) Y-->U; 288 (6) M-->G; 290 (8) M==>E; 292 (4) Y==>U; 293 (19) Y-->F; 309 (12) M-->A; 358 (1) T==>C; 371 (1) C==>T; 598 (1) C==>T; 615 (1) T-->C; 644 (1) T-->C; 696 (1) T==>C; 794 (1) G==>A; 847 (1) T-->C; 913 (1) A-->G; 1200 (1) C==>T; 1398 (1) T-->C; 1547 (1) A-->C; 1749 (1) T==>C; 1761 (1) C==>T; 1887 (1) C==>T; 1907 (1) C-->T; 1925 (1) T==>C; 1997 (1) T==>C; 2198 (1) A-->G; 2236 (1) T-->C; 2522 (1) C-->A; 2553 (1) T-->C.
DELTRAN: 12 (4) J-->F; 13 (1) H-->G; 14 (1) B-->A; 36 (2) S==>U; 52 (14) U==>G; 75 (2) M==>K; 84 (4) Y-->U; 85 (5) J-->E; 95 (8) U-->M; 102 (6) M==>S; 106 (5) F==>K; 109 (4) Y==>U; 123 (10) U==>K; 135 (2) I==>K; 192 (18) A==>S; 193 (15) A==>P; 194 (9) A-->J; 230 (10) U==>K; 231 (6) G-->A; 281 (2) K-->M; 288 (2) M-->K; 290 (6) K==>E; 292 (4) Y==>U; 358 (1) T==>C; 371 (1) C==>T; 451 (1) C-->T; 496 (1) T-->C; 515 (1) A-->G; 543 (1) A-->C; 566 (1) T-->C; 575 (1) T-->C; 587 (1) A-->G;

598 (1) C==>T; 623 (1) T-->C; 641 (1) A-->G; 659 (1) A-->G; 686 (1) C-->T; 695 (1) C-->T; 696 (1) T==>C; 764 (1) C-->T; 794 (1) G==>A; 1200 (1) C==>T; 1327 (1) C-->T; 1548 (1) T-->A; 1749 (1) T==>C; 1761 (1) C==>T; 1887 (1) C==>T; 1925 (1) T==>C; 1997 (1) T==>C.

Branch 24
ACCTRAN: 2 (2) K-->I; 11 (3) G-->D; 12 (5) F-->A; 32 (10) U-->K; 51 (4) Y==>U; 63 (6) Y==>S; 71 (6) A==>G; 75 (2) K==>I; 95 (12) M==>A; 97 (8) K==>S; 109 (4) U==>Q; 135 (14) K==>Y; 137 (5) K-->F; 141 (12) Y==>M; 148 (9) Y==>P; 194 (6) J==>P; 209 (18) S==>A; 212 (4) E==>I; 219 (18) G==>Y; 225 (7) P-->I; 245 (10) A==>K; 257 (20) U-->A; 258 (4) E-->A; 261 (8) Q-->Y; 265 (5) F==>A; 268 (2) E==>G; 283 (9) P-->Y; 284 (8) E-->M; 289 (6) Y==>S; 290 (4) E==>A; 292 (8) U==>M; 307 (8) Q-->Y; 375 (1) T-->C; 387 (1) T==>C; 395 (1) A==>G; 440 (1) C==>T; 441 (1) A==>C; 450 (1) A==>G; 477 (1) A==>C; 509 (1) T==>C; 540 (1) A==>G; 551 (1) A==>G; 594 (1) C==>T; 596 (1) G-->A; 620 (1) T==>C; 629 (1) A==>G; 632 (1) C==>T; 653 (1) G-->A; 656 (1) T==>C; 671 (1) C==>A; 677 (1) T==>C; 737 (1) C==>T; 740 (1) T-->C; 758 (1) T==>C; 1073 (1) G==>A; 1549 (1) T==>C; 1731 (1) G-->A; 1783 (1) G==>A; 2132 (1) T==>C.
DELTRAN: 51 (4) Y==>U; 63 (6) Y==>S; 71 (6) A==>G; 75 (2) K==>I; 95 (12) M==>A; 97 (8) K==>S; 109 (4) U==>Q; 113 (4) Q-->U; 135 (14) K==>Y; 141 (12) Y==>M; 148 (9) Y==>P; 194 (6) J==>P; 209 (16) Q==>A; 212 (4) E==>I; 219 (15) J==>Y; 245 (10) A==>K; 265 (5) F==>A; 268 (2) E==>G; 289 (6) Y==>S; 290 (4) E==>A; 292 (8) U==>M; 387 (1) T==>C; 395 (1) A==>G; 440 (1) C==>T; 441 (1) A==>C; 450 (1) A==>G; 455 (1) A-->C; 477 (1) A==>C; 509 (1) T==>C; 540 (1) A==>G; 551 (1) A==>G; 594 (1) C==>T; 620 (1) T==>C; 629 (1) A==>G; 632 (1) C==>T; 656 (1) T==>C; 671 (1) C==>A; 677 (1) T==>C; 737 (1) C==>T; 758 (1) T==>C; 1073 (1) G==>A; 1547 (1) A-->C; 1549 (1) T==>C; 1783 (1) G==>A; 2132 (1) T==>C.

Branch 25
ACCTRAN: 3 (3) G-->D; 4 (3) L-->I; 5 (4) H-->D; 6 (3) Q==>T; 7 (4) G-->K; 9 (6) K==>Q; 10 (5) L-->Q; 12 (2) H-->J; 13 (1) H-->I; 52 (11) U-->J; 79 (5) A-->F; 84 (4) Y-->U; 85 (3) M-->J; 94 (3) M-->P; 95 (7) M-->F; 102 (2) M-->K; 113 (4) U-->Y; 134 (9) Y-->P; 143 (9) Y-->P; 147 (4) Y-->U; 148 (9) Y-->P; 149 (6) A-->G; 150 (6) Q-->K; 154 (4) A-->E; 170 (2) S-->U; 173 (4) Y-->U; 177 (5) P-->U; 218 (4) Y-->U; 243 (3) F-->I; 253 (6) P-->J; 257 (4) U-->Q; 263 (5) A-->F; 266 (10) S-->I; 273 (4) Y-->U; 274 (2) G-->I; 287 (5) U-->P; 288 (4) E-->A; 319 (1) A==>T; 412 (1) G==>T; 421 (1) C==>A; 422 (1) T==>A; 428 (1) C==>A; 430 (1) A==>C; 437 (1) C==>T; 482 (1) C==>T; 531 (1) T-->A; 533 (1) C==>A; 545 (1) A==>T; 588 (1) C==>T; 593 (1) C==>T; 630 (1) T==>G; 636 (1) A==>G; 637 (1) C==>T; 638 (1) T==>C; 671 (1) C-->A; 737 (1) C==>T; 743 (1) C==>T; 794 (1) G-->A; 939 (1) A==>C; 943 (1) T==>C; 998 (1) T-->C; 1109 (1) C-->A; 1144 (1) C==>T; 1175 (1) T==>C; 1239 (1) C-->T; 1369 (1) A-->T; 1392 (1) C-->T; 1399 (1) A-->G; 1575 (1) C-->A; 1761 (1) C-->T; 1783 (1) G-->A; 1914 (1) A-->G; 2078 (1) C-->T; 2101 (1) A-->G; 2504 (1) C-->T; 2525 (1) T-->C; 2553 (1) T-->C.
DELTRAN: 3 (1) E-->D; 6 (3) Q==>T; 9 (2) J==>L; 319 (1) A==>T; 359 (1) C-->T; 412 (1) G==>T; 421 (1) C==>A; 422 (1) T==>A; 428 (1) C==>A; 430 (1) A==>C; 437 (1) C==>T; 482 (1) C==>T; 533 (1) C==>A; 545 (1) A==>T; 588 (1) C==>T; 593 (1) C==>T; 630 (1) T==>G; 636 (1) A==>G; 637 (1) C==>T; 638 (1) T==>C; 713 (1) C-->T; 737 (1) C==>T; 743 (1) C==>T; 939 (1) A==>C; 943 (1) T==>C; 1109 (1) C-->A; 1144 (1) C==>T; 1175 (1) T==>C.

Branch 26
ACCTRAN: 2 (4) G-->K; 6 (2) T-->V; 8 (2) O-->Q; 352 (1) G==>A; 368 (1) C==>A; 373 (1) T==>C; 408 (1) A==>G; 410 (1) C-->T; 411 (1) C==>T; 414 (1) C==>T; 415 (1) C==>T; 440 (1) C==>A; 442 (1) C==>T; 451 (1) C==>T; 453 (1) C==>T; 470 (1) A==>G; 493 (1) C==>T; 494 (1) C==>A; 496 (1) T==>C; 528 (1) C==>T; 536 (1) C==>T; 572 (1) C==>T; 573 (1) A==>C; 575 (1) T==>C; 586 (1) C==>T; 621 (1) A-->C; 644 (1) T-->C; 650 (1) C==>T; 656 (1) T-->C; 659 (1) G-->A; 660 (1) T==>G; 674 (1) C-->T; 677 (1) T==>C; 695 (1) C==>T; 696 (1) T==>C; 728 (1) C==>T.
DELTRAN: 2 (4) G-->K; 14 (1) B-->A; 52 (5) U-->P; 53 (4) E-->A; 76 (4) Y-->U; 94 (3) M-->P; 95 (5) U-->P; 102 (2) M-->K; 104 (2) I-->G; 134 (9) Y-->P; 143 (6) Y-->S; 148 (4) Y-->U; 170 (2) S-->U; 180 (3) M-->P; 218 (4) Y-->U; 261 (3) M-->P; 266 (10) S-->I; 274 (2) G-->I; 294 (3) M-->P; 352 (1) G==>A; 368 (1) C==>A; 373 (1) T==>C; 396 (1) A-->G; 408 (1) A==>G; 410 (1) C-->T; 411 (1) C==>T; 414 (1) C==>T; 415 (1) C==>T; 440 (1) C==>A; 442 (1) C==>T; 451 (1) C==>T; 453 (1) C==>T; 470 (1) A==>G; 493 (1) C==>T; 494 (1) C==>A; 496 (1) T==>C; 512 (1) C-->T; 528 (1) C==>T; 531 (1) T-->A; 532 (1) T-->C; 536 (1) C==>T; 572 (1) C==>T; 575 (1) T==>C; 586 (1) C==>T; 623 (1) T==>C; 650 (1) C==>T; 660 (1) T==>G; 671 (1) C-->A; 677 (1) T==>C; 695 (1) C==>T; 696 (1) T==>C; 728 (1) C==>T; 740 (1) C-->T; 1369 (1) A-->T; 1392 (1) C-->T; 1732 (1) A-->G; 1761 (1) C-->T; 2525 (1) T-->C.

Branch 27
ACCTRAN: 22 (9) Y-->P; 23 (12) M-->A; 24 (20) Y-->E; 33 (2) S-->Q; 36 (9) P-->Y; 39 (11) P-->E; 41 (6) S-->Y; 43 (15) P-->A; 49 (2) M-->K; 51 (12) U==>I; 52 (9) J==>A; 75 (16) U-->E; 80 (15) P-->A; 82 (24) A-->Y; 85 (9) J==>A; 95 (5) F-->A; 116 (5) P-->K; 121 (12) M-->A; 123 (10) U-->K; 124 (5) U-->P; 127 (6) G-->A; 129 (10) A-->K; 133 (5) K-->P; 135 (9) A-->J; 136 (2) M-->K; 141 (14) Y-->K; 144 (6) A-->G; 146 (3) P-->S; 150 (6) K-->E; 154 (4) E-->I; 163 (4) Y-->U; 167 (5) F-->K; 173 (10) U-->K; 177 (4) U-->Y; 178 (24) A-->Y; 181 (14) Y-->K; 182 (12) M-->Y; 183 (1) A-->B; 192 (12) M-->Y; 193 (8) M-->U; 194 (6) J-->P; 195 (6) J-->P; 196 (15) A-->P; 197 (9) A-->J; 198 (4) A-->E; 207 (9) Y-->P; 211 (8) A-->I; 212 (20) E-->Y; 213 (20) A-->U; 225 (5) A-->F; 230 (12) M-->A; 233 (24) Y-->A; 235 (9) P-->Y; 241 (9) P-->Y; 242 (9) P-->Y; 245 (18) A-->S; 247 (9) Y-->P; 249 (4) U-->Y; 253 (1) J-->I; 262 (14) Y-->K; 263 (5) F-->K; 264 (4) Y-->U; 267 (5) U-->P; 273 (4) U-->Q; 284 (9) P-->Y; 285 (8) I-->Q; 287 (5) P-->K; 289 (14) Y-->K; 290 (10) K-->A; 292 (19) Y-->F; 293 (12) M-->A; 308 (6) A-->G; 309 (12) M-->A; 452 (1) C-->G; 621 (1) C-->G; 784 (1) T-->G; 785 (1) G-->T; 786 (1) T-->G; 1210 (1) C-->A; 1286 (1) C==>T; 1368 (1) C==>A; 1411 (1) T-->A; 1452 (1) A==>C; 1471 (1) C==>T; 1534 (1) G==>A; 1546 (1) T==>C; 1572 (1) C==>T; 1573 (1) C==>T; 1702 (1) A==>C; 1768 (1) C==>T; 1771 (1) A-->G; 1913 (1) A-->G; 1980 (1) A==>G; 2019 (1) C==>T; 2095 (1) G==>A; 2360 (1) C==>T; 2377 (1) A-->G; 2432 (1) A==>C; 2493 (1) T-->A.

DELTRAN: 4 (4) M-->I; 5 (5) I-->D; 6 (2) T-->V; 9 (5) L-->Q; 10 (7) J-->Q; 51 (16) Y==>I; 52 (15) P==>A; 84 (4) Y-->U; 85 (9) J==>A; 794 (1) G-->A; 1239 (1) C-->T; 1286 (1) C==>T; 1327 (1) C-->T; 1368 (1) C==>A; 1426 (1) T==>C; 1452 (1) A==>C; 1471 (1) C==>T; 1534 (1) G==>A; 1546 (1) T==>C; 1572 (1) C==>T; 1573 (1) C==>T; 1702 (1) A==>C; 1768 (1) C==>T; 1783 (1) G-->A; 1898 (1) A-->T; 1980 (1) A==>G; 2019 (1) C==>T; 2095 (1) G==>A; 2236 (1) C-->T; 2360 (1) C==>T; 2432 (1) A==>C.

Branch 28
ACCTRAN: 1 (8) A==>I; 2 (7) K==>R; 4 (12) I==>U; 5 (17) D==>U; 8 (3) Q==>T; 9 (5) Q-->L; 10 (9) Q==>H; 11 (3) G==>J; 13 (8) I==>Q; 23 (3) M==>P; 25 (4) Y==>U; 30 (4) Y==>U; 31 (11) U==>J; 33 (6) S-->Y; 41 (18) S==>A; 43 (9) P-->Y; 45 (5) P-->U; 49 (12) M-->Y; 69 (10) A==>K; 70 (5) A==>F; 71 (10) A==>K; 77 (5) P-->U; 94 (9) P==>Y; 97 (6) K==>E; 99 (5) A==>F; 102 (2) K==>I; 106 (10) A==>K; 110 (16) E==>U; 111 (14) E==>S; 117 (10) A-->K; 121 (12) M==>Y; 125 (15) P==>A; 127 (9) G==>P; 131 (9) Y==>P; 151 (5) P==>U; 152 (15) A==>P; 153 (1) Q-->P; 157 (5) U-->P; 169 (10) A==>K; 170 (4) U==>Y; 175 (4) Y==>U; 179 (24) A==>Y; 180 (9) P==>Y; 182 (2) M==>K; 190 (14) Y==>K; 191 (20) Y-->E; 192 (12) M-->A; 193 (12) M-->A; 194 (9) J-->A; 195 (9) J-->A; 201 (5) A-->F; 208 (4) A-->E; 210 (16) Q-->A; 212 (4) E==>A; 219 (9) J==>A; 223 (19) Y==>F; 227 (19) F==>Y; 230 (12) M-->Y; 231 (15) A==>P; 232 (4) A==>E; 239 (4) A==>E; 248 (9) Y==>P; 252 (4) Y==>U; 257 (1) Q-->P; 266 (3) I==>F; 267 (4) U-->Y; 268 (4) A-->E; 270 (5) P==>K; 274 (12) I==>U; 275 (9) A==>J; 285 (3) I==>F; 299 (8) Q-->Y; 307 (9) Y==>P; 309 (8) M==>U; 636 (1) G-->C; 638 (1) C-->A; 639 (1) G-->C; 794 (1) A-->G; 939 (1) C==>G; 994 (1) G==>A; 1052 (1) T==>C; 1071 (1) T==>C; 1074 (1) T-->A; 1082 (1) T==>C; 1091 (1) T==>C; 1106 (1) A-->G; 1239 (1) T-->C; 1327 (1) T-->C; 1347 (1) C-->A; 1370 (1) A==>C; 1426 (1) C-->T; 1734 (1) A==>G; 1749 (1) T==>C; 1861 (1) T==>A; 1898 (1) T-->A; 1947 (1) A==>G; 2079 (1) C==>T; 2113 (1) T==>C; 2236 (1) T==>C; 2484 (1) C==>T.
DELTRAN: 1 (8) A==>I; 2 (7) K==>R; 4 (8) M==>U; 5 (12) I==>U; 7 (4) G-->K; 8 (3) Q==>T; 10 (2) J==>H; 11 (3) G==>J; 13 (9) H==>Q; 23 (5) K==>P; 25 (4) Y==>U; 30 (4) Y==>U; 31 (3) M==>J; 36 (3) S-->P; 41 (6) G==>A; 69 (10) A==>K; 70 (5) A==>F; 71 (10) A==>K; 75 (8) M-->U; 77 (5) P-->U; 94 (9) P==>Y; 97 (6) K==>E; 99 (5) A==>F; 102 (2) K==>I; 106 (5) F==>K; 110 (10) K==>U; 111 (14) E==>S; 121 (12) M==>Y; 125 (10) K==>A; 127 (5) K==>P; 131 (9) Y==>P; 135 (8) I-->A; 151 (5) P==>U; 152 (15) A==>P; 153 (1) Q-->P; 157 (5) U-->P; 169 (10) A==>K; 170 (4) U==>Y; 175 (4) Y==>U; 179 (14) K==>Y; 180 (9) P==>Y; 182 (2) M==>K; 190 (5) P==>K; 210 (8) I-->A; 212 (4) E==>A; 219 (9) J==>A; 223 (19) Y==>F; 227 (14) K==>Y; 230 (4) U-->Y; 231 (9) G==>P; 232 (4) A==>E; 239 (4) A==>E; 248 (5) U==>P; 252 (4) Y==>U; 257 (1) Q-->P; 266 (3) I==>F; 270 (5) P==>K; 274 (12) I==>U; 275 (9) A==>J; 285 (3) I==>F; 293 (2) K-->M; 307 (9) Y==>P; 309 (10) K==>U; 939 (1) C==>G; 994 (1) G==>A; 1005 (1) C-->T; 1052 (1) T==>C; 1071 (1) T==>C; 1082 (1) T==>C; 1091 (1) T==>C; 1106 (1) A-->G; 1347 (1) C-->A; 1370 (1) A==>C; 1575 (1) C-->A; 1734 (1) A==>G; 1749 (1) T==>C; 1771 (1) G-->A; 1861 (1) T==>A; 1947 (1) A==>G; 2078 (1) C-->T; 2079 (1) C==>T; 2101 (1) A-->G; 2113 (1) T==>C; 2484 (1) C==>T; 2504 (1) C-->T.

Branch 29
ACCTRAN: 2 (1) E-->D; 3 (10) T-->J; 4 (8) D-->L; 5 (2) G-->I; 6 (8) I-->Q; 9 (2) K==>M; 18 (4) Y==>U; 19 (12) M-->A; 23 (8) M==>U; 24 (16) E-->U; 31 (20) A==>U; 33 (6) Y-->S; 34 (6) S-->Y; 37 (24) A==>Y; 38 (24) A==>Y; 41 (20) Y-->E; 43 (5) K-->P; 45 (4) Y-->U; 49 (24) A-->Y; 51 (4) Y-->U; 52 (20) Y==>E; 53 (24) Y-->A; 54 (24) Y-->A; 55 (18) S-->A; 56 (18) S-->A; 57 (12) M-->A; 64 (16) Q-->A; 66 (24) Y-->A; 69 (5) A-->F; 70 (5) A==>F; 76 (4) Y-->U; 80 (18) G==>Y; 81 (4) U-->Y; 86 (4) Y-->U; 87 (12) M-->A; 95 (24) A-->Y; 97 (10) A-->K; 99 (8) I-->A; 100 (24) A==>Y; 101 (24) A==>Y; 102 (3) S-->P; 105 (24) Y-->A; 113 (3) M-->P; 114 (8) S-->K; 121 (10) A-->K; 123 (10) U==>K; 124 (4) Y-->U; 125 (8) S-->K; 135 (10) A==>K; 145 (1) G-->F; 150 (1) Q==>P; 151 (8) U-->M; 159 (20) A==>U; 164 (24) A-->Y; 166 (6) A==>G; 173 (12) M-->Y; 178 (3) M-->J; 179 (10) A-->K; 182 (8) M==>U; 188 (6) S-->Y; 189 (6) S-->Y; 190 (8) M-->U; 191 (15) A==>P; 192 (4) A==>E; 200 (6) S-->Y; 201 (5) U-->P; 203 (3) S-->P; 204 (6) G-->A; 208 (24) Y==>A; 212 (20) Y-->E; 213 (18) S-->A; 216 (8) I-->Q; 219 (2) Q-->S; 220 (6) A==>G; 227 (2) I-->K; 235 (15) A-->P; 245 (19) Y-->F; 253 (12) Y-->M; 261 (12) A-->M; 262 (14) Y==>K; 268 (9) S-->J; 269 (4) Y-->U; 270 (9) Y-->P; 277 (4) Y-->U; 278 (2) M-->K; 279 (10) Q==>G; 281 (7) M-->F; 283 (3) S==>P; 284 (2) M==>K; 285 (2) M-->K; 288 (8) M-->E; 292 (1) E-->F; 300 (4) A==>E; 308 (24) A==>Y; 310 (1) A-->B; 313 (1) G-->A; 317 (1) A-->C; 320 (1) C-->T; 332 (1) A-->G; 375 (1) C-->A; 377 (1) G-->A; 392 (1) A==>T; 413 (1) C-->A; 421 (1) C==>A; 437 (1) C==>T; 467 (1) C==>T; 495 (1) C-->A; 501 (1) A==>C; 519 (1) A==>T; 533 (1) C==>A; 536 (1) C==>T; 550 (1) C-->A; 563 (1) T-->C; 587 (1) A-->C; 620 (1) C-->T; 632 (1) C==>T; 637 (1) C==>T; 650 (1) A-->C; 665 (1) C-->A; 674 (1) C-->T; 695 (1) C==>T; 713 (1) T-->C; 714 (1) A==>G; 728 (1) C==>T; 740 (1) T-->C; 755 (1) C==>A; 758 (1) T==>C; 761 (1) A-->C; 803 (1) C-->T; 813 (1) T-->C; 825 (1) T-->C; 845 (1) A==>G; 874 (1) A-->G; 904 (1) A-->G; 939 (1) T-->A; 1007 (1) C==>T; 1044 (1) A-->G; 1082 (1) A-->T; 1144 (1) A-->T; 1145 (1) G-->A; 1191 (1) T-->C; 1201 (1) C==>T; 1211 (1) G-->A; 1212 (1) T-->C; 1243 (1) C-->A; 1246 (1) A-->C; 1253 (1) C==>T; 1311 (1) C-->A; 1341 (1) C-->T; 1367 (1) C==>T; 1373 (1) G-->A; 1377 (1) T-->A; 1393 (1) T==>A; 1394 (1) T==>C; 1398 (1) C-->A; 1419 (1) C-->A; 1432 (1) T-->A; 1449 (1) C-->A; 1460 (1) C==>T; 1494 (1) G-->A; 1513 (1) T-->C; 1550 (1) G-->A; 1566 (1) A-->C; 1572 (1) C==>T; 1575 (1) C-->A; 1589 (1) T-->C; 1618 (1) A-->C; 1678 (1) A-->G; 1702 (1) T-->A; 1728 (1) G-->A; 1735 (1) C-->A; 1761 (1) C==>T; 1898 (1) C-->A; 1904 (1) C-->A; 1938 (1) G-->A; 1945 (1) C==>T; 1953 (1) C-->T; 2064 (1) C-->T; 2070 (1) C-->T; 2089 (1) A-->C; 2114 (1) T-->A; 2133 (1) G-->A; 2156 (1) C-->A; 2160 (1) A-->G; 2236 (1) A-->C; 2250 (1) T-->C; 2340 (1) C-->T; 2433 (1) C-->A; 2467 (1) T==>C; 2500 (1) A==>T; 2503 (1) T-->A; 2524 (1) T-->A; 2525 (1) T==>A; 2537 (1) T-->C; 2587 (1) T-->C; 2692 (1) T==>C.
DELTRAN: 1 (4) A-->E; 2 (1) E-->D; 9 (2) K==>M; 18 (4) Y==>U; 23 (8) M==>U; 31 (20) A==>U; 33 (6) Y-->S; 37 (24) A==>Y; 38 (24) A==>Y; 41 (2) G-->E; 45 (4) Y-->U; 51 (4) Y-->U; 52 (16) U==>E; 53 (15) P-->A; 54 (4) E-->A; 69 (5) A-->F; 70 (5) A==>F; 76 (4) Y-->U; 80 (14) K==>Y; 100 (24) A==>Y; 101 (24) A==>Y; 102 (3) S-->P; 105 (6) G-->A; 121 (5) F-->K; 123 (10) U==>K; 133 (2) I-->G; 135 (2) I==>K; 145 (1) G-->F; 150 (1) Q==>P; 151 (3) P-->M; 157 (15) U-->F; 159 (20) A==>U; 166 (6) A==>G; 177 (3) M-->P; 180 (3) M-->P; 182 (8) M==>U; 188 (4) U-->Y; 189 (4) U-->Y; 190 (5) P-->U; 191 (11) E==>P; 192 (4) A==>E; 208 (20) U==>A; 216 (6) K-->Q; 219 (2) Q-->S; 220 (6) A==>G; 253 (3) P-->M; 262 (14) Y==>K; 269 (4) Y-->U; 277 (4) Y-->U; 278 (2) M-->K; 279 (10) Q==>G; 281 (3) I-->F; 283 (5) U==>P; 284 (5) P==>K; 288 (8) M-->E; 294 (6) G-->A; 300 (4) A==>E; 308 (24) A==>Y; 392 (1) A==>T; 421 (1) C==>A; 437 (1) C==>T; 467 (1) C==>T; 495 (1) C-->A; 501 (1) A==>C; 519 (1)

A==>T; 533 (1) C==>A; 536 (1) C==>T; 620 (1) C-->T; 632 (1) C==>T; 637 (1) C==>T; 650 (1) A-->C; 665 (1) C-->A; 695 (1) C==>T; 714 (1) A==>G; 725 (1) C-->T; 728 (1) C==>T; 749 (1) C-->T; 755 (1) C==>A; 758 (1) T==>C; 761 (1) A-->C; 845 (1) A==>G; 1007 (1) C==>T; 1091 (1) C-->T; 1144 (1) A-->T; 1201 (1) C==>T; 1253 (1) C==>T; 1367 (1) C==>T; 1393 (1) T==>A; 1394 (1) T==>C; 1460 (1) C==>T; 1494 (1) G-->A; 1572 (1) C==>T; 1761 (1) C==>T; 1945 (1) C==>T; 2467 (1) T==>C; 2500 (1) A==>T; 2525 (1) T==>A; 2553 (1) C-->T; 2692 (1) T==>C.

Branch 30
ACCTRAN: 1 (4) A-->E; 4 (3) A-->D; 5 (1) F-->G; 6 (7) I-->B; 9 (3) K-->H; 19 (12) Y-->M; 25 (6) S-->Y; 34 (18) A-->S; 36 (6) S==>Y; 43 (4) G-->K; 47 (1) A==>B; 71 (8) I-->A; 72 (24) Y-->A; 75 (12) M==>Y; 77 (12) A-->M; 81 (20) A-->U; 88 (4) A==>E; 99 (16) I==>Y; 103 (8) M-->E; 106 (24) A==>Y; 109 (6) S-->Y; 110 (20) A==>U; 111 (12) A==>M; 115 (5) A-->F; 116 (9) G-->P; 117 (15) A-->P; 119 (6) G-->A; 123 (4) Y-->U; 127 (2) M-->K; 133 (8) I-->A; 136 (10) A-->K; 144 (12) Y-->M; 150 (8) Q-->Y; 151 (4) Y-->U; 153 (24) Y-->A; 157 (24) Y-->A; 158 (8) Y==>Q; 162 (12) A-->M; 167 (12) A-->M; 168 (12) M-->Y; 169 (24) A==>Y; 170 (6) Y-->S; 177 (12) M==>Y; 178 (12) M==>Y; 180 (10) F-->P; 182 (12) A-->M; 184 (24) A-->Y; 185 (24) A==>Y; 188 (6) S==>M; 189 (18) S==>A; 190 (12) M==>A; 201 (4) Y-->U; 203 (6) S==>Y; 204 (18) G==>Y; 209 (8) Q==>Y; 213 (6) Y-->S; 217 (24) A==>Y; 219 (4) M-->Q; 221 (24) Y-->A; 222 (24) A-->Y; 223 (24) Y==>A; 224 (3) I-->F; 226 (12) Y-->M; 227 (2) G-->I; 228 (1) B-->A; 230 (18) G-->Y; 231 (14) G==>U; 234 (8) Q-->Y; 238 (6) S-->Y; 248 (12) A-->M; 251 (18) A-->S; 254 (24) Y-->A; 257 (4) Y-->U; 258 (24) Y-->A; 265 (3) I-->F; 266 (12) Y-->M; 271 (2) S-->U; 274 (6) A-->G; 279 (8) Q-->Y; 281 (8) M==>U; 283 (6) Y-->S; 284 (12) Y-->M; 285 (12) Y-->M; 287 (6) S==>Y; 288 (12) M==>Y; 289 (24) A==>Y; 292 (4) A-->E; 293 (12) A==>M; 294 (6) G-->A; 295 (10) A-->K; 296 (24) Y-->A; 303 (24) A-->Y; 304 (20) A-->U.
DELTRAN: 1 (4) A-->E; 36 (4) U==>Y; 47 (1) A==>B; 75 (8) M==>U; 88 (4) A==>E; 99 (16) I==>Y; 106 (19) F==>Y; 110 (10) K==>U; 111 (8) E==>M; 115 (5) A-->F; 150 (8) Q-->Y; 158 (8) Y==>Q; 167 (5) A-->F; 169 (5) A==>F; 177 (12) M==>Y; 178 (12) M==>Y; 185 (24) A==>Y; 188 (6) S==>M; 189 (18) S==>A; 190 (12) M==>A; 203 (6) S==>Y; 204 (9) G==>P; 209 (8) Q==>Y; 217 (24) A==>Y; 223 (19) Y==>F; 230 (4) U-->Y; 231 (14) G==>U; 279 (4) Q-->U; 281 (8) M==>U; 283 (2) U-->S; 284 (3) P-->M; 287 (4) U==>Y; 288 (8) M==>U; 289 (14) K==>Y; 293 (7) F==>M; 294 (6) G-->A.

Branch 31
ACCTRAN: 2 (3) E-->B; 23 (12) M-->A; 24 (20) E-->Y; 34 (6) S-->Y; 39 (6) G==>M; 43 (10) K-->U; 44 (15) A-->P; 46 (12) A==>M; 55 (6) S==>Y; 56 (6) S==>Y; 57 (12) M==>Y; 58 (24) A==>Y; 59 (20) A==>U; 60 (15) A==>P; 61 (9) A==>J; 62 (4) A-->E; 64 (8) Q==>Y; 67 (24) A==>Y; 80 (6) G==>A; 81 (4) U-->Y; 82 (10) A-->K; 87 (12) M==>Y; 88 (8) E==>M; 89 (12) A==>M; 90 (12) A==>M; 91 (12) A==>M; 92 (12) A==>M; 96 (1) A-->B; 102 (18) S-->A; 103 (4) E-->A; 105 (24) Y-->A; 110 (4) U-->Y; 113 (12) M-->A; 114 (18) S==>A; 115 (7) F==>M; 116 (3) P-->S; 123 (8) U-->M; 125 (18) S==>A; 127 (10) K==>A; 134 (24) Y==>A; 141 (12) Y==>M; 145 (18) G==>Y; 147 (24) Y==>A; 158 (16) Q==>A; 165 (24) Y==>A; 170 (13) S-->F; 173 (7) M-->F; 176 (24) A==>Y; 181 (12) M-->Y; 183 (1) A-->C; 200 (6) S-->Y; 208 (12) Y-->M; 214 (24) A-->Y; 215 (12) Y==>M; 216 (8) I==>A; 219 (4) Q-->U; 227 (2) I-->K; 231 (4) U-->Y; 241 (4) G-->K; 242 (10) A==>K; 257 (8) U-->M; 268 (6) S-->M; 271 (4) U-->Y; 281 (4) U-->Y; 283 (6) S-->M; 292 (6) E-->K.
DELTRAN: 6 (7) I-->B; 24 (16) E-->U; 39 (6) G==>M; 44 (4) A-->E; 46 (12) A==>M; 55 (6) S==>Y; 56 (6) S==>Y; 57 (12) M==>Y; 58 (12) A==>M; 59 (12) A==>M; 60 (12) A==>M; 61 (9) A==>J; 64 (8) Q==>Y; 67 (24) A==>Y; 80 (6) G==>A; 87 (12) M==>Y; 88 (8) E==>M; 89 (12) A==>M; 90 (12) A==>M; 91 (4) A==>E; 92 (4) A==>E; 105 (24) Y-->A; 114 (13) S==>F; 115 (5) F==>K; 123 (5) U-->P; 125 (13) S==>F; 127 (10) K==>A; 134 (24) Y==>A; 141 (12) Y==>M; 145 (12) G==>S; 147 (4) Y==>U; 153 (14) Y-->K; 158 (10) Q==>G; 162 (5) A-->F; 165 (14) Y==>K; 176 (5) A==>F; 200 (6) S-->Y; 215 (12) Y==>M; 216 (8) I==>A; 221 (24) Y-->A; 229 (5) F==>A; 241 (4) G-->K; 242 (10) A==>K; 257 (5) U-->P; 268 (6) S-->M; 292 (6) E-->K; 304 (16) A-->Q.

Branch 32
ACCTRAN: 3 (3) T-->Q; 10 (1) L==>M; 19 (12) M==>Y; 20 (24) A==>Y; 25 (9) Y==>P; 39 (12) M==>Y; 46 (3) M==>P; 75 (4) Y-->U; 77 (7) M==>F; 88 (12) M==>Y; 89 (8) M==>U; 90 (8) M==>U; 93 (4) A==>E; 133 (18) A==>S; 141 (6) M==>G; 167 (7) M-->F; 169 (19) Y-->F; 175 (4) Y==>U; 184 (24) Y==>A; 204 (9) Y-->P; 212 (4) Y==>U; 213 (9) S==>J; 215 (7) M==>F; 222 (24) Y-->A; 223 (5) A-->F; 226 (12) M==>Y; 243 (10) A==>K; 253 (9) Y-->P; 261 (10) A==>K; 268 (2) M==>K; 279 (4) Y-->U; 288 (4) Y-->U.
DELTRAN: 3 (3) T-->Q; 10 (1) L==>M; 19 (12) M==>Y; 20 (24) A==>Y; 25 (9) Y==>P; 39 (12) M==>Y; 46 (3) M==>P; 77 (7) M==>F; 88 (12) M==>Y; 89 (8) M==>U; 90 (8) M==>U; 93 (4) A==>E; 117 (5) K-->P; 133 (10) I==>S; 141 (6) M==>G; 175 (4) Y==>U; 180 (3) M-->P; 184 (24) Y==>A; 212 (4) Y==>U; 213 (9) S==>J; 214 (9) P-->Y; 215 (7) M==>F; 224 (3) I-->F; 226 (4) U==>Y; 243 (10) A==>K; 253 (9) Y-->P; 261 (10) A==>K; 268 (2) M==>K; 295 (10) A-->K; 313 (1) A-->G; 377 (1) A-->G; 404 (1) C-->T; 413 (1) A-->C; 550 (1) A-->C; 570 (1) A-->T; 708 (1) C-->T; 713 (1) C-->T; 740 (1) C-->T; 813 (1) C-->T; 825 (1) C-->T; 998 (1) C-->T; 1145 (1) A-->G; 1191 (1) C-->T; 1212 (1) C-->T; 1311 (1) A-->C; 1419 (1) A-->C; 1432 (1) A-->T; 1513 (1) C-->T; 1550 (1) A-->G; 1589 (1) C-->T; 1938 (1) A-->G; 2114 (1) A-->T; 2133 (1) A-->G; 2250 (1) C-->T; 2484 (1) C-->T; 2587 (1) C-->T.

Appendix H

Specimens examined for interspecific analysis

Specimens for interspecific analyses (Chapter 5) were examined from four university collections: Texas Tech University (TTU), the University of Texas at Arlington (UTA), the University of Texas at El Paso (UTEP), and the Texas Natural History Collection, Texas Memorial Museum at the University of Texas at Austin (TNHC). Specimens with an * were used for both gross morphological measurements and linear cranial measurements, otherwise specimens were only used for gross morphological measurements.

Crotalus lepidus: TNHC 3283, 3680, 3973, 4045, 7574*, 7694*, 7700*, 7859*, 7894*, 7955*, 7957, 7960*, 4987*, 8002*, 8040*, 8041*, 8108*, 8119*, 8208, 8340*, 8383*, 11608*, 11733, 12798*, 12806*, 14985*, 15293, 15335*, 18568*, 18569*, 18570*, 20145, 20146*, 25914*, 29186*, 29876*, 31108, 32546, 33010*, 33011*, 33888*, 33938*, 54050*.

Crotalus molossus: THNC 1013*, 1382*, 1903*, 2504*, 2873*, 3078*, 3285*, 3520, 3887*, 4257*, 7125*, 7806, 7893*, 7991*, 8039, 8223*, 8404*, 11736*, 11828-29, 11830*, 12509*, 12593*, 12632, 12792, 12794*, 12887*, 12934*, 12936*, 12969*, 14986, 14987*, 14988*, 14989*, 20148*, 21742*, 25481*, 25670, 47649*, 48806*, 54078*, 60216*.

Crotalus viridis: TNHC 1376*, 7118, 7342, 10193, 10423*, 11498*, 11553*, 15300, 29061*, 29064*, 29065*, 32256*, 60212, 60213*; TTU 42*, 1405*, 1490*, 1491*, 1496*, 1497*, 1564*, 1567*, 1585*, 2148*, 2150*, 2152*, 2153*, 2161*, 2162*, 2251*, 2463*, 2726*, 2915*, 2916*, 2918*, 2926*, 3016*, 3120A*, 3120B*, 3121*, 3177*, 3178*, 3188*, 3443*, 3444*, 9701*, 9702*; UTEP 66, 67, 69, 312, 781, 1040, 1725, 1758, 1852, 1853, 3980 ,3026, 6116, 9027, 11007, 11008, 11451, 12320, 13825, 14090, 14147, 15429, 18826.

Crotalus willardi: UTA 5640*, 5641*, 6124*, 6125*, 7162*, 8688*, 9356*, 9862*, 13035*, 17846*, 17847*, 17848*, 17849*, 18361*, 18362*, 18363*, 18423*, 18424*, 18425*, 19413*, 21922*, 22526*, 25101*, 26532*, 26536*, 32081*, 34548*, 34549*, 35591*, 39020*, 39021*, 39080*.

Sistrurus catenatus: TNHC 989, 8570, 32257, 33884, 55941; UTA 2610*, 6809*, 9284*, 11283*, 11286*, 11289*, 11291*, 11297*, 11314*, 11315*, 11316*, 11318*, 11321*, 11325*, 11327*, 11328*, 11340*, 11341*, 11346*, 11357, 11358*, 11359*, 11361, 12676*, 12677*, 12678*, 12679*, 12680*, 12681*, 12682*, 12683*, 12684*, 12772*, 14082*, 14083*, 16393*, 22372*, 40817*, 40831*, 40832*.

Sistrurus miliarius: TNHC 5149, 7451, 8568-9, 12255, 12274, 12318, 14142, 17538-40, 19811-2, 21931, 24773, 28780-82, 29238-40, 56076-81, 57021; UTA 1288*, 1332*, 2293*, 2294*, 2337*, 2338*, 2423*, 2503*, 6776*, 6777*, 10999*, 12776*, 14615*, 15671*, 15676*, 16868*, 18029*, 18364*, 25121*, 25122*, 26539*, 26540*, 28259*, 28810*, 30732*, 32165*, 34172*, 35207*, 35208*, 35209*, 35210*, 35211*, 35212*, 35213*, 35215*, 40389*, 40390*, 44582*, 44583*, 44588*.

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